TRI-TROPHIC ANALYSES OF RICE, THE SUGARCANE BORER, AND PUTATIVE BIOLOGICAL CONTROL AGENTS

A Dissertation

by

JIALE LV

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2008

Major Subject: Entomology

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Approved by:

Chair of Committee,	Lloyd T. Wilson
Committee Members,	Julio S. Bernal
	Michael T. Longnecker
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ABSTRACT

Tri-trophic Analyses of Rice, the Sugarcane Borer, and Putative Biological Control
Agents. (December 2008)
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A three-year field experiment was conducted to evaluate the tolerance and compensatory response of rice (*Oryza sativa* L.) to injury caused by the sugarcane borer, *Diatraea saccharalis* (F.). Two mechanisms of within-plant tolerance/compensation were observed. Stem injured plants produced ca. 0.69 more tillers than uninjured plants, while tillers with leaf and leaf sheath injury produced larger panicles, up to 39.5% and 21.0% heavier than uninjured tillers, when injury occurred at 3rd tiller stage and at panicle differentiation, respectively.

A 2-year field cage experiment was conducted to determine the biological control potential of *Cotesia flavipes* (Cameron) against the sugarcane borer on rice. The effective search rate was 49 cm^2 ground area (2.2 tillers) $parasitoid^{-1}$ day^{-1}. A cohort-based age-structured model was developed to simulate the population dynamics and economic value of the sugarcane borer and *C. flavipes* in rice, as affected by overwintering larval density, timing and rate of parasitoid aerial release, and year-to-year climate (temperature and rainfall). The results suggest *C. flavipes* was most effective when released during the 1st sugarcane borer generation. The maximum simulated economic benefit (\$112.05 ha^{-1}) was ca. 7.8% of that provided by insecticide-based control. The inability of *C. flavipes* to provide economic control in temperate-subtropical areas is due to its high rearing cost, a low effective search rate, a low maximum rate of parasitism per female, and both spatial and temporal asynchrony of parasitoid emergence with the larval hosts. The biocontrol capability of *Trichogramma galloi* Zucchi was also simulated. The maximum economic benefit provided by *T. galloi* was \$1128.75 ha^{-1}, ca. 79.0% of that provided by insecticide-based control.

Theoretical analyses were conducted to estimate the effectiveness of augmentative releases, using data from previous studies of parasitism of lepidopteran pests by hymenopteran parasitoids with host and parasitoid density as factors. The maximum daily parasitism per female was highest for parasitoids that attack exposed larvae, followed by parasitoids that attack eggs, semi-exposed larvae, and concealed larvae. Simulation analyses were conducted to estimate the population dynamics and economic value of *D. saccharalis*, herein used as a model host, and each of 5 parasitoid categories (solitary parasitoids that attack eggs, exposed larvae, and semi-exposed larvae, gregarious parasitoids that attack eggs and concealed larvae) in rice, as affected by overwintering larval density, timing of parasitoid release, and year-to-year climate. Among the 13,500 simulations that were conducted, 480 (3.6%) provided a greater economic value than insecticide-based control. All 480 simulations were obtained using solitary parasitoids that attack exposed or semi-exposed larvae. Solitary egg parasitoids provided an average of 42.2% of the economic value provided by insecticide-based control when released 30 days after planting. Gregarious parasitoids that attack eggs or concealed larvae provided almost no positive economic benefit. For parasitoid species that do not overwinter successfully in areas where they are released or that exhibit temporal or spatial asynchrony with their host early in the spring, our results suggest augmentative biological control is only effective for solitary parasitoids that attack either exposed or semi-exposed larvae, with current rearing, shipping and release costs.

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CHAPTER I

INTRODUCTION

Rice is an annually grown graminaceous grass, belonging to the tribe Oryzeae and the family Poaceae. While the origin of rice is not known, the cultivation of rice was initiated in the river valleys of South and Southeast Asia ca. 8,000-15,000 years ago (De Datta 1981, Normile 2004). Rice is the major food crop in Asia, and provides over one-fifth of all calories consumed by humans globally. The worldwide annual production of rice rose from ca. 350 million tonnes in the 1980's to over 600 million tonnes in 2007 (IRRI 2007). The annual production in the U.S. is ca. 10 million tonnes, contributing 1.6% of world rice production, and 80.8% of the total production in North and Central America. The rice producing states in the U.S. are Arkansas, California, Florida, Louisiana, Mississippi, Missouri, and Texas. Rice is cultivated on ca. 87,500 ha. in southeastern Texas (Stansel and Tate 2005). Yields average ca. 7,700 kg ha^{-1} (Stansel and Tate 2005), with individual field yields as high as ca. 17,000 kg ha^{-1} (L. T. Wilson personal communication). The rice industry contributes ca. $490 million to the gross state farm product, and ranks as the 9th largest agricultural commodity in Texas (Falconer 2008).

This dissertation follows the style of Environmental Entomology.

Insect pests are major constraints that limit world rice yields. Cramer (1967), Pathak and Dhaliwal (1981), and Oerke (1994) reported insect pests cause ca. 26.7%, 24%, and 20.7% of rice yield loss worldwide. More than 800 species of rice insect pests have been identified worldwide (Grist and Lever 1969). However, only a small number are of major economic importance. Grist and Lever (1969) listed 28 important rice insect pest species in Asia, 9 in Australia, 15 in Africa, and 13 in North and Central America. Way (2003) listed common arthropod rice pests in U.S., including insect species in 17 genus.

The two most important insect pests in southern U.S. rice production states are the rice water weevil, *Lissorhoptrus oryzophilus* Kushel (Coleoptera: Curculionidae), and the rice stink bug, *Obealus pugnax* (F.) (Hemiptera: Pentatomidae). More recently, stem borers have increased in abundance and have reached key pest status. Way et al. (2006) reported stem borer injury reducing yield by up to 60% in untreated rice fields in Ganado, Texas. The stem borer complex in southern U.S. rice producing states includes the sugarcane borer, *Diatraea saccharalis* (F.) (Lepidoptera: Crambidae), the Mexican rice borer, *Eoreuma loftini* (Dyar) (Lepidoptera: Pyralidae), and the rice stalk borer, *Chilo plejadellus* Zincken (Lepidoptera: Pyralidae). The sugarcane borer has been the predominant stem borer species in rice in both Texas and Louisiana, since shortly following its introduction to Louisiana in the 19th century (Bowling 1967, Williams et al. 1969). The Mexican rice borer was first discovered in Texas in 1980 and now causes yield loss across the Texas ricebelt (Reay-Jones et al. 2005). Although the importance of the Mexican rice borer continues to increase, Way et al. (2006) reported ca. 60% of stem borers recovered in Ganado, TX were sugarcane borers. The rice stalk borer is far less abundant than the other two stem borer species.

The principal cultivated hosts of the sugarcane borer are sugarcane (*Saccharum officinarum* L.), corn (*Zea mays* L.), rice, and sorghum (*Sorghum* spp.). This species also feeds on several wild grass species, such as Johnson grass (*Sorghum halapense* L.) and bull grass (*Paspalum* spp.) (Hensley 1971). Eggs of this species are laid on leaves, and first and second instar larvae feed on leaves. Third instar larvae begin to burrow through the stems. Burrowing injury retards plant growth and reduces yield. In the Upper Gulf Coast region of the U.S., there are 3-4 generations of the sugarcane borer per year. Overwintering larvae terminate diapause in April, and adults emerging from overwintering larvae produce 1st generation eggs in late April and May (White et al. 2004).

Larval injury to sugarcane is reported to be responsible for reduced juice quality and reduced vegetative bud production (Hensley 1971). Reagan et al. (1972) and Schexnayder et al. (2001) reported the sugarcane borer is responsible for 90% of the total insect damage to sugarcane in Louisiana. Research on sugarcane borer injury to rice is limited. However, considerable research has been conducted on injury to rice by other species of borers that are ecologically and taxonomically similar to the sugarcane borer. Injury to rice by striped stem borer, *Chilo suppressalis* (Walker), and yellow stem borer, *Scirpophaga incertulas* (Walker), results in both whiteheads, whose grains have been completely destroyed, and reduced grain weight of apparently healthy panicles. For every percent of whiteheads, a 1-3% loss in yield occurs (Pathak and Patanakamjorn 1971, Chaudhary et al. 1984).

Patanakamjorn and Pathak (1967) reported plant height, stem diameter, and length and width of the flag leaf were positively correlated with number of eggs laid by rice striped borer (*Chilo suppressalis* Walker) and yellow stem borer (*Tryporyza incertulas* Walker) in rice. In addition, resistant cultivars possess tight leaf sheaths that totally cover the internodes, whereas susceptible cultivars have loose leaf sheaths that partially cover the internodes. Tight leaf sheaths are believed to prevent newly hatched larvae from feeding on the inner part of the leaf sheath before boring into the stem. Crop stage appears to be another important factor contributing to borer host plant resistance. Pathak and Patanakamjorn (1971) showed some rice cultivars exhibit resistance to injury by striped stem borer and yellow stem borer during the entire season, while others exhibit resistance during either early or later stages of crop growth, but not both. These results indicate either the mechanisms of resistance or the impact of injury caused by stem borers at different crop stages may differ.

Biological control of the sugarcane borer using predators is mainly through natural control. Bessin et al. (1990) reported arthropod predation reduces sugarcane borer injured internodes by 13.4-21.7%, and reduces the sugarcane borer population by 1.9 fold. Parasitoids of the sugarcane borer have been observed in several families of Hymenoptera and one family of Diptera. Previous research suggests parasitoids can inflict a high level of mortality upon sugarcane borer populations. Browning and Melton (1987) recorded *Trichogramma fuentesi* Torre (Hymenoptera: Trichogrammatidae) parasitized 78.7% of sugarcane borer eggs in sugarcane fields in the Lower Rio Grande Valley of Texas. Parra and Zucchi (2004) studied the efficacy of biocontrol in sugarcane in Brazil when using a number of *Trichogramma* species in combination with *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae), a larval parasitoid, and found the highest sugarcane borer population reduction (60.2%) occurring with *Trichogramma galloi* Zucchi and *C. flavipes*. Alam (1980) reported the introduction of *C. flavipes* and *Lixophaga diatraeae* (Townsend) (Diptera: Tachinidae), two larval parasitoids, successfully reduced sugarcane borer injury to sub-economic levels in Barbados. The successful control of the sugarcane borer using *C. flavipes* in sugarcane has also been documented in the Rio Grande Valley of Texas (Meagher et al. 1998).

Trichogramma fuentesi, *T. galloi*, and *L. diatraeae* coevolved with the sugarcane borer, while *C. flavipes* lacks a long-term association with this species. *Cotesia flavipes* is indigenous to the Indo-Australian region, where its hosts are within the *Chilo* genus. Studies of *C. flavipes* as a natural enemy of *Chilo* pests in rice were conducted in Japan (Smith et al. 1993) and China (Song et al. 1996, Zhu et al. 1999, You et al. 2000, Li et al. 2005). However, these studies mainly focused on natural control, and did not evaluate the ability of *C. flavipes* to prevent economic loss. While *C. flavipes* is documented to have a major impact on sugarcane borer populations in perennial hosts, such as sugarcane, which are temporally stable, its ability to control stem borer pests on ephemeral host crops, such as rice, is poorly understood. White and Reagan (1999) reviewed results from *C. flavipes* releases in the Rio Grande Valley, and concluded this parasitoid was best adapted to control sugarcane borer populations in perennial agriculture systems in subtropical areas, with 3 to 4 years required for introduced parasitoids to reduce and maintain population densities below economic injury levels.

This dissertation has three primary objectives: 1) to quantify the response of three rice cultivars at different crop growth stages to sugarcane borer injury; a component of this objective is directed at identifying the impact of cultivar and climatic variables (rain and wind) on sugarcane borer survival, injury, and damage, 2) to determine the potential value of *C. flavipes* as an augmentatively released agent for biocontrol of the sugarcane borer on rice. Life table parameters for both the sugarcane borer and *C. flavipes*, obtained from published data and focused experiments presented herein, were incorporated into a simulation model of seasonal population dynamics. A range of overwintering sugarcane borer larval densities, and timings and rates of *C. flavipes* release were simulated. A cost/benefit analysis was conducted by combining estimates of yield loss and parasitoid rearing and release costs. A secondary objective is to examine the potential for using *T. galloi* to provide economic control of the sugarcane borer, and 3) to estimate the economic benefit obtained from augmentative release of hymenopteran parasitoids having solitary or gregarious oviposition strategies, that attack different stages of the sugarcane borer.

CHAPTER II

TOLERANCE AND COMPENSATORY RESPONSE OF RICE TO THE SUGARCANE BORER (LEPIDOPTARA: CRAMBIDAE) INJURY*

Introduction

The principal cultivated hosts of the sugarcane borer, *Diatraea saccharalis* (F.), are sugarcane, corn, rice, and sorghum (Hensley 1971). This insect also feeds on several wild grass species, such as Johnson grass (*Sorghum halepense* L.), Dallis grass (*Paspalum dilatatum* Poir), and panic grass (*Panicum* spp.) (Bessin and Reagan 1990). Eggs of this species are laid on leaves, and first and second instar larvae feed on leaves. Third instar larvae begin to burrow into the stems. Burrowing injury retards plant growth and reduces yield.

In the Upper Gulf Coast Region of the U.S., there are 3-4 generations of the sugarcane borer per year. Overwintering larvae terminate diapause in April, and adults emerging from overwintering larvae produce 1st generation eggs in late April and May (White et al. 2004). Larval injury to sugarcane is reported to be responsible for reduced juice quality and reduced vegetative bud production (Hensley 1971). Reagan et al.

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(1972) and Schexnayder et al. (2001) reported the sugarcane borer is responsible for 90% of the total insect damage to sugarcane in Louisiana. The sugarcane borer has been the predominant stem borer species in rice in both Texas and Louisiana, since shortly following its introduction to Louisiana in the 19th century (Bowling 1967, Williams et al. 1969). Another important stem borer pest, the Mexican rice borer, *Eoreuma loftini* (Dyar), was first discovered in Texas in 1980 (Reay-Jones et al. 2005), and is now a major pest throughout all of the Texas ricebelt. The occurrence of both species has increased in recent years. Way et al. (2006) reported stem borer injury resulted in rice yield losses of up to 60%. Among all stem borers recovered from their field sampling, ca. 60% were sugarcane borers.

The use of resistant cultivars is an important management tool for the sugarcane borer on sugarcane. Bessin et al. (1991) reported resistant sugarcane cultivars reduced adult emergence by 40%. Hensley (1971) showed yield loss of different sugarcane cultivars due to sugarcane borer injury ranged from a low of 14.6% to a high of 28.6%. Kyle and Hensley (1970) reported the major mechanism involved in the resistance of ‘NCo 310’ to the sugarcane borer was antibiosis expressed as a high level of mortality to small larvae before they tunneled into stalks, while oviposition preference was not a significant factor. Coburn and Hensley (1972) concluded antibiosis was largely of a mechanical nature, and was mostly conferred by leaf sheaths that are tightly appressed to the stems. Martin et al. (1975) used a durometer to measure rind hardness and demonstrated a highly significant negative correlation between sugarcane internode hardness and the percentage of internodes that were penetrated by larvae ($r = -0.97$).

These studies suggest biochemical and physical characteristics inherent to different cultivars may be responsible for different levels of borer resistance in sugarcane.

Research on sugarcane borer injury to rice is limited. However, considerable research has been conducted on injury to rice by other species of borers, which are ecologically and taxonomically similar to the sugarcane borer. Injury to rice by striped stem borer, *Chilo suppressalis* (Walker), and yellow stem borer, *Scirpophaga incertulas* (Walker), results in both whiteheads, whose grains have been completely destroyed, and reduced grain weight of apparently healthy panicles. For every percent of whiteheads, a 1-3% loss in yield occurs (Pathak and Patanakamjorn 1971, Chaudhary et al. 1984). Patanakamjorn and Pathak (1967) reported numbers of eggs laid by striped stem borer and yellow stem borer were positively correlated with rice plant height, stem diameter, and length and width of the flag leaf. In addition, resistant cultivars possess tight leaf sheaths that totally cover the internodes, whereas susceptible cultivars have loose leaf sheaths that partially cover the internodes. Tight leaf sheaths are believed to prevent newly hatched larvae of these species from feeding on the inner part of leaf sheaths before boring into stems. Jodon and Ingram (1948) reported a positive correlation between stem diameter and infestation for a borer complex comprised of five species in Asia. Israel (1967) reported rice cultivars with greater plant height, larger leaf area, and greater tiller numbers are more susceptible to stem borers than other cultivars.

Crop stage appears to be another important factor affecting the resistance of host plants to borers in both sugarcane and rice. Long and Concienne (1964) showed the most important period for sugarcane borer control is in July and August in sugarcane, when larvae of the second and third generations injure millable internodes. Control measures directed against later generations do not increase sugarcane yield. Pathak and Patanakamjorn (1971) showed some rice cultivars exhibit resistance to injury by striped stem borer and yellow stem borer during the entire season, while others exhibit resistance during either early or later stages of crop growth, but not both. These results indicate either the mechanisms of resistance or the impact of injury caused by stem borers at different crop stages may differ.

Tolerance is the ability of host plants to suffer limited injury and resultant damage in the presence of an insect population sufficiently large to severely damage susceptible hosts (Painter 1958). Compensation is the ability of host plants to partially or completely replace yield loss caused by pest injury (Trumble et al. 1993). Compensation can occur both within a single plant and between adjoining plants. For example, decreased leaf area can result in a decrease in feedback inhibition and elevated rates of photosynthesis on a per unit leaf area basis. Similarly, injury to the roots or stem tissue can reduce the ability of a plant or tiller to capture light and nutrients, resulting in increased availability of these resources to neighboring uninjured plants or tillers. Trumble et al. (1993) referred to these phenomena as a relief from environmental pressure. Rubia et al. (1996) tracked the assimilation of CO_2 and the allocation of photosynthate in rice plants with leaf injury using ^{14}C, and reported the photosynthetic rate of healthy leaves on injured tillers was greater than that of healthy leaves on healthy tillers. Research conducted in transplanted low-density hill production systems suggests rice can partially or fully compensate for stem injury by producing a greater number of reproductive tillers and producing heavier panicles on neighboring healthy tillers (Akinsola 1984, Gill et al. 1992, Islam and Karim 1997, 1999, Jiang and Cheng 2003).

The impact of tolerance and compensation cannot be easily separated. The main objective of this research is directed at quantifying the combined tolerance and compensatory response of three rice cultivars at different crop growth stages to sugarcane borer injury, from here forward referred to as compensation. A secondary objective is directed at identifying the impact of cultivar and climatic variables (rain and wind) on sugarcane borer survival, injury, and damage.

Methods and Materials

Field Experiment Design. A field experiment was conducted during 2004, 2005, and 2006 at the Texas A&M AgriLife Research and Extension Center at Beaumont. The soil at Beaumont is a fine montmorillonite and thermic Entic Pelludert (Chen et al. 1989). Fields were planted on April 18, April 22, and April 19 in 2004, 2005, and 2006, respectively, using a 0.18 m-row spacing.

A 3 × 3 Latin Square design was used each year, with each main plot 8.3 m × 8.4 m, separated by 1.8 m wide lanes. Crop growth stage was the main plot factor. Each plot contained 18 completely randomized split plots, consisting of all possible combination of 3 cultivars (Cocodrie, Francis, and Jefferson) and 6 sugarcane borer larval densities. Cocodrie and Francis were planted at a rate of 120 kg seed ha^{-1}, while Jefferson was planted at 144 kg seed ha^{-1}. The planting rate differed among cultivars because Jefferson has a lower germination rate. The plant density was thinned to 20 plants per meter-row (111.1 plants m^{-2}) at the four-leaf stage, prior to the initiation of tillering. Each split plot was 2.4 m × 6 rows, separated from adjacent split plots within the same row by a 0.6 m blank area, and separated from split plots in adjacent rows by two blank rows. For each split plot, the central 1 m × 4 rows were sampled, with the outer rows and the end of each split plot used as buffers.

The previously cited references suggest plant height, tiller density, and stem diameter affect injury to rice by other borer species. Three cultivars used in this experiment were chosen to represent a range of these phenotypic traits. Cocodrie (Cypress // L-202 / Tebonnet) is moderately tall, produces the highest number of tillers, and has the smallest stem diameter. Francis (Lebonnet / Dawn // Starbonnet / Lagrue) is the tallest, produces the fewest tillers, and has a moderate stem diameter. Jefferson (Rosemont // Vista / Lebonnet) is the shortest, produces an intermediate number of tillers, and has the largest stem diameter (Lv personal observation).

Three crop growth stages were selected, corresponding to 3rd tiller (ca. 45 days after seeding), panicle differentiation (ca. 75 days after seeding), and heading (ca. 100 days after seeding). The three stages represented a period of rapid tiller production and vegetative growth, a period of transition from vegetative to reproductive development, and a period of rapid grain filling, respectively. With the exception of 3rd tiller stage, which was estimated by visual observation, the timing of each crop growth stage were estimated using the Rice Development Advisory Program (Wilson et al. 2004), which is a heat driven rice phenology model, with the climatic records for the three rice seasons obtained from the database described in Wilson et al. (2005).

The six densities for this experiment were established by placing egg masses on the youngest expanded leaves, mimicking adult oviposition preference (Dale 1994), in the center meter of plants in one of the two center rows of each split plot. Zero, 1, 2, 3, 4, and 5 (Density 0, 1, 2, 3, 4, and 5) equally spaced tillers were selected and a piece of wax paper containing ca. 75 eggs that were darkened and ready to hatch were attached using a paper clip. Egg masses used in this experiment were obtained from a USDA-ARS colony maintained by Dr. W. H. White in Houma, LA. The USDA colony has been maintained in the lab since 1989, with wild moths introduced in 2000 and 2006 from a sugarcane field in Houma.

Injury and Yield Assessment. Each split plot was monitored ca. 10-12 days after infestation. The number of injured tillers per row was recorded, and paper clips and wax paper were removed. Previous research has shown 10 day-old larvae have developed to the 3rd instar and have begun to injure rice stems (King et al. 1975). As a result, sampling 10-12 days after egg attachment provided an estimate of the maximum number of injured tillers. Karate Z (150 ml active ingredient ha^{-1}, 500 L water ha^{-1}, 20 kpa) was applied using a Gilmour 030PEXG Greenlawn 9.5 L sprayer 30 days after each of the first two releases to prevent emergence and reproduction of moths and prevent further injury. Pesticide was not applied following the third release because the sugarcane borers had not emerged prior to the harvest.

Fields were harvested on August 11, August 23, and August 17 in 2004, 2005, and 2006, respectively. Three sampling methods were used at harvest to estimate larval injury, tillering, and yield. The first method recorded the grain mass of each split plot. This method provided data on the unit area yield as affected by cultivar, stage, and initial sugarcane borer density.

The second method used the initially infested row as the sampling unit. Tillers were categorized as uninjured (without any observable stem injury) or stem injured. The number of tillers and the total yield of each category were recorded. This method provided data on survival of injured tillers, unit area tiller density, and the average yield per injured and uninjured tiller, as affected by cultivar, stage, and larvae density remaining on the initially infested row.

The third method used a plant or a tiller as the sampling unit. This method provided data for use in estimating the impact of injury on subsequent tillering by injured and non-injured plants, and the yield of each injured and uninjured tiller. In 2004, each plant of the initially infested rows of “Density 1” of Francis was numbered and harvested separately. Each plant was identified as either uninjured (U) or stem injured (I). Tillers in each plant were categorized into 3 groups: uninjured tillers in uninjured plants (UU), uninjured tillers in stem injured plants (UI), and injured tillers in stem injured plants (II). The number of tillers and the grain mass (0% moisture) of each tiller category in each plant were recorded. Only one cultivar was selected during the first year because of limited availability of labor. Francis was selected because the least amount of information was available about the stem borer resistance of this newly released cultivar (Way et al. 2006).

In 2005 and 2006, the initially infested rows of “Density 2” were selected instead of “Density 1”, because injury to stems in the later two years was lower than recorded during the first year. Instead of classifying plants as uninjured or stem injured, plants were classified into three categories: uninjured (U), leaf and leaf sheath injured (L), and stem injured (S), with the third category usually including plants with leaf and leaf sheath injury as well. Tillers were correspondingly categorized into 6 groups: uninjured tillers in uninjured plants (UU), uninjured tillers in leaf and leaf sheath injured plants (UL), leaf and leaf sheath injured tillers in leaf and leaf sheath injured plants (LL), uninjured tillers in stem injured plants (US), leaf and leaf sheath injured tillers in stem injured plants (LS), and stem-injured tillers in stem injured plants (SS). Unlike the 2004 sampling, the grain mass of each tiller was recorded separately.

Analyses and Statistics. Four categories of response variables were analyzed: 1) sugarcane borer injury (number of injured tillers 10-12 days after infestation, and number of stem-injured tillers that survived to harvest), 2) tillering (tiller density per m^2 and number of tillers per plant), 3) yield per tiller (mean grain yield per uninjured tiller, mean grain yield per injured tiller, and grain yield per tiller), and 4) grain yield per m^2.

The majority of data were analyzed using analyses of variances (ANOVAs) and second order polynomial regressions. The main factors used in each analysis are listed in Table 2.1. The ANOVAs evaluate the effect of main factors and interactions on the response variables. Main factors or interactions with $P < 0.05$ are considered

Table 2.1. Main factors used in ANOVAs and regression analyses of number of injured tillers, number of stem-injured tillers, number of tillers per plant, tiller density m^{-2}, grain yield per tiller, mean grain yield per uninjured tiller, mean grain yield per injured tiller, and yield m^{-2}

Response Variable	Sampling Time	Sampling Unit	Data Source	Main Factors							
				Year	Cultivar	Stage	Initial Egg Density	Plant injury category	Tiller injury category	Proportion of Injured Tillers	Proportion of Stem-injured tillers
Number of Injured Tillers	10-12 days after infestation	Split Plot	2004-2006	A, R[a]	A, R	A, R	A, R	-	-	-	-
Number of Stem-injured tillers at Harvest	Harvest	Initially Infested Row[b]	2004-2006	A, R	A, R	A, R	A, R	-	-	R	-
Number of Tillers per Plant	Harvest	Plant	2004	-	-	A	-	A	-	-	-
	Harvest	Plant	2005-2006	A	A	A	-	A	-	-	-
Tiller Density m^{-2}	Harvest	Initially Infested Row	2004-2006	A, R	A, R	A, R	A	-	-	R	R
Yield per Tiller	Harvest	Tiller	2004	-	-	A	-	A	A	-	-
	Harvest	Tiller	2005, 2006	A	A	A	-	A	A	-	-
Mean Grain Yield per Uninjured Tiller	Harvest	Initially Infested Row	2004-2006	A	A	A	A	-	-	-	-
Mean Grain Yield per Injured Tiller	Harvest	Initially Infested Row	2004-2006	A	A	A	A	-	-	-	-
Yield m^{-2}	Harvest	Split Plot	2004-2006	A, R	A, R	A, R	A	-	-	R	R

[a] "A" refers to the factors used in ANOVAs, and "R" refers to the independent variables used in the regression analyses.

[b] Initially infested row refers to the row with egg masses artificially attached.

to be statistically significant for all ANOVAs. For ANOVAs using each split plot or the initially infested row as the sampling unit, statistically significant main factors and interactions that explained more than 5% of variability are discussed in detail. For ANOVAs using plant or tiller as sampling units, all main factors and interactions that are statistically significant are discussed in detail. ANOVA results are expressed as $\bar{x} \pm s.d.$ Tukey's HSD test is used for mean separations. Second order polynomial regressions are used to derive injury response functions for the number of injured tillers and the number of stem-injured tillers that survived to harvest, each as a function of initial egg density. Second order multivariate regressions are used to derive injury response functions for normalized tiller density, yield per tiller, and yield per m^2, each as a function of the proportion of tillers that were injured, the proportion of stems that were injured that survived to harvest, and the degree-days (> 10ºC from planting), referring to the physiological age of rice (Wu and Wilson 1998) when injury occurred. Independent variables with $p < 0.05$ are considered to be statistically significant. Each response variable was normalized with respect to the corresponding uninjured treatment mean. For example, the normalized tiller density of each split plot equals the tiller density divided by the mean tiller density of uninjured split plots for the corresponding cultivar and year. Similarly, the proportion of injured tillers and the proportion of stem-injured tillers that survived to harvest were calculated as the number of injured tillers and the number of stem-injured tillers that survived to harvest, each divided by the corresponding mean tiller density of uninjured split plots.

For each cultivar and each crop growth stage, a 3-way chi-square test was conducted to compare the tillering of plants either adjacent to injured plants or to uninjured plants. The three dimensions of the chi-square tests are the number of tillers per plant (x), the number of tillers on neighboring plant (y), and whether the plant is injured or uninjured (z). Tillering data obtained from the first sampling method were used in this analysis, where the observed value, O_{ijk}, equals the number of uninjured or injured plants (k = "U" or "I") having i tillers, with a neighboring plant having j tillers among all sampled plots (n). The expected value (E_{ijk}) was estimated using Eq. (2.1a). The chi-square value (χ^2) of the 3-way test was calculated using Eq. (2.1b), where X, Y, Z are the total number of cells of each of the three dimensions, and the degree of freedom for the chi-square test equals (X-1)(Y-1)(Z-1).

$$E_{ijk} = \frac{\sum x_i \cdot \sum y_j \cdot \sum z_k}{n^2} \tag{2.1a}$$

$$\chi^2 = \sum \frac{(O_{ijk} - E_{ijk})^2}{E_{ijk}} \tag{2.1b}$$

Results and Discussion

Sugarcane Borer Injury to Tillers. The number of injured tillers was significantly affected by year, stage, cultivar, density, and the year × stage, year × cultivar, year × density, and stage × cultivar × density interactions. The number of stem-injured tillers that survived to harvest was significantly affected by the same main effects and interactions, and the stage × cultivar interaction (Table 2.2). A greater number of tillers was injured in 2004 (49.8 ± 10.9 m^{-2}) and 2005 (48.1 ± 10.9 m^{-2}) than in 2006

Table 2.2. ANOVAs of number of injured tillers, number of stem-injured tillers, tiller density m^{-2}, mean grain yield per uninjured tiller, mean grain yield per injured tiller, and yield m^{-2}

Source of Variances	df	Number of Injured Tillers			Number of Stem-injured tillers			Tiller Density m^{-2}			Mean Grain Yield per Uninjured Tiller			Mean Grain Yield per Injured Tiller			Yield m^{-2}		
		F	P > F	% Explained Variability	F	P > F	% Explained Variability	F	P > F	% Explained Variability	F	P > F	% Explained Variability	F	P > F	% Explained Variability	F	P > F	% Explained Variability
Year	2	43.0	~ 0	6.8	102.7	~ 0	28.2	50.4	~ 0	11.6	173.6	~ 0	39.3	27.3	~ 0	12.2	49.4	~ 0	10.7
Stage	2	25.9	~ 0	4.1	27.6	~ 0	7.6	8.2	0.004	1.9	10.0	0.002	2.3	1.2	0.328	0.5	8.0	0.005	1.7
Year × Stage	4	4.1	0.021	1.3	3.9	0.025	2.1	4.3	0.018	2.0	6.9	0.003	3.1	2.4	0.100	2.2	4.6	0.014	2.0
Row	2	0.5	0.614	0.1	1.5	0.253	0.4	0.2	0.842	0.0	0.6	0.553	0.1	0.4	0.691	0.2	2.6	0.109	0.6
Column	2	3.5	0.060	0.6	0.2	0.850	0.0	0.3	0.741	0.1	0.6	0.547	0.1	0.1	0.886		2.1	0.164	0.4
Error (1)	14																		
Cultivar	2	3.5	0.031	0.2	14.4	~ 0	2.1	104.2	~ 0	0.1	48.0	~ 0	0.1	17.8	~ 0	0.1	28.9	~ 0	0.4
Year × Cultivar	4	5.3	~ 0	0.7	6.9	~ 0	2.0	5.6	~ 0	1.6	12.7	~ 0	1.6	2.5	0.044	3.1	8.5	~ 0	1.5
Stage × Cultivar	4	2.1	0.084	0.3	3.5	0.008	1.0	1.5	0.213	21.5	1.0	0.411	7.9	4.3	0.002	6.8	0.9	0.445	7.3
Year × Stage × Cultivar	8	1.5	0.151	0.4	1.9	0.055	1.1	2.4	0.017	2.3	0.7	0.732	4.2	2.0	0.051	1.9	2.0	0.046	4.2
Density	5	390.1	~ 0	67.4	40.9	~ 0	15.1	15.8	~ 0	0.6	6.7	~ 0	0.3	2.3	0.047	3.3	15.4	~ 0	0.5
Year × Density	10	5.0	~ 0	1.7	11.0	~ 0	8.1	4.7	~ 0	2.0	6.5	~ 0	0.4	1.0	0.426	3.0	4.8	~ 0	2.0
Cultivar × Density	10	1.2	0.316	0.4	0.6	0.852	0.4	1.5	0.123	8.2	0.5	0.896	2.7	1.2	0.276	2.2	1.7	0.088	9.6
Year × Cultivar × Density	20	0.9	0.561	0.6	1.40	0.122	2.1	1.0	0.522	4.9	0.5	0.966	5.3	0.7	0.834	2.0	1.1	0.310	6.0
Stage × Density	8	1.8	0.079	0.5	1.1	0.340	0.7	1.4	0.217	1.6	1.0	0.462	0.4	0.9	0.550	2.4	1.9	0.057	2.1
Year × Stage × Density	16	1.0	0.439	0.6	0.6	0.847	0.8	0.9	0.552	2.0	1.0	0.418	0.8	1.0	0.446	2.7	0.6	0.883	2.9
Stage × Cultivar × Density	16	1.9	0.021	1.0	1.2	0.271	1.4	0.4	0.987	1.1	0.6	0.872	0.6	1.2	0.269	1.3	0.5	0.939	1.9
Year × Stage × Cultivar × Density	32	0.8	0.747	0.9	0.5	0.986	1.2	0.9	0.580	1.5	0.9	0.694	1.4	0.5	0.991	3.1	0.9	0.561	1.2
Error (2)	324																		

(24.0 ± 10.8 m^{-2}). In contrast, a greater number of stems was injured in 2004 (43.7 ± 9.5 m^{-2}), than in 2005 (11.0 ± 7.4 m^{-2}) and 2006 (11.4 ± 5.2 m^{-2}). The artificial infestations represent low to high densities compared to natural infestation in Texas (Way et al. 2006). Low natural infestations were observed in this experiment. The number of injured tillers in "Density 0" were 0.09 ± 0.18 m^{-2}, 0.27 ± 0.41 m^{-2}, and 0.11 ± 0.13 m^{-2} in 2004, 2005, and 2006, respectively, and the number of stem-injured tillers were 0.71 ± 0.92 m^{-2}, 0.62 ± 0.82 m^{-2}, and 0.69 ± 1.00 m^{-2} in 2004, 2005, and 2006, respectively. The number of stem-injured tillers at harvest and the number of injured tillers 10-12 days after egg attachment provided a relative estimate of the proportion of injury to stems, which was the greatest in 2004 (0.87), followed by 2006 (0.48) and 2005 (0.22). An estimated 12.4%, 13.6%, and 8.4% of tillers and ca. 10.9%, 3.1%, and 4.0% of stems were injured in 2004, 2005, and 2006, respectively.

Survival to the end of the 1st instar, estimated as the ratio of the number of injured tillers and the number of eggs infesting the plants, was 0.10 (2004), 0.02 (2005), and 0.03 (2006) at 3rd tiller, 0.23 (2004), 0.20 (2005), and 0.13 (2006) at panicle differentiation, and 0.20 (2004), 0.21 (2005), and 0.12 (2006) at heading. Survival from the end of the first instar to the early 3rd instar, the latter occurring prior to the larvae fully entering the stems, was estimated as the ratio of the number of tillers with stem injury and the number of injured tillers, and was 0.64 (2004), 0.11 (2005), and 0.58 (2006) at 3rd tiller, 0.95 (2004), 0.21 (2005), and 0.37 (2006) at panicle differentiation, and 1.00 (2004), 0.40 (2005), and 0.40 (2006) at heading. Survival to the end of the 1st instar was lower at 3rd tiller in comparison to the two latter stages. A putative reason for low survival during this crop growth stage is the lower leaf and tiller densities. First instars spin silk and disperse with the wind by “ballooning” (Berger 1988). Low leaf and tiller densities result in a greater chance for larvae failing to attach to leaves or tillers, and falling into water during dispersal. The lower survival to the end of the 1st instar in 2006 appears to have been caused by rainfall occurring within 5 days after each of the two latter infestations, while the lower survival from the end of the first instar to the early 3rd instar in 2005 and 2006 appears to have been caused by rainfall occurring 6-20 days after each of the two latter infestations. The impact of rainfall on survival was estimated by regressing survival as a function of two rainfall covariates, one for rainfall occurring within 5 days after each infestation (Eq. 2.2a) and one for rainfall occurring 6-20 days after each infestation (Eq. 2.2b).

$$R_{1-5} = \sum_{i=1}^{5} \left(\frac{5-i+1}{5} \right) \cdot r_i \tag{2.2a}$$

$$R_{6-20} = \sum_{i=6}^{20} \left(\frac{20-i+1}{15} \right) \cdot r_i \tag{2.2b}$$

where:

R_{1-5} = Covariate for rainfall occurring within 5 days after each infestation (cm)

R_{6-20} = Covariate for rainfall occurring 6-20 days after each infestation (cm)

i = i^{th} day after each infestation

r_i = Daily rainfall (cm) on the i^{th} day after each infestation

Significant regressions were observed for survival to the end of the 1st instar and survival from the end of the first instar to the early 3rd instar, with each negatively related to rainfall (Fig. 2.1). In contrast, significant relationships were not observed between survival and rainfall when injury occurred during the 3rd tiller stage. Previous research has shown rainfall dislodges lepidopteran eggs and early instar larvae. Kobori and Amano (2003) found the survival of diamondback moth, *Plutella xylostella* (L.), (Lepidoptera: Plutellidae) eggs dislodged by rainfall is ca. 0.20 on cabbage, while the survival of dislodged 1st and 2nd instar larvae was 0.00. Bonhof and Overholt (2001) reported significant reduction of maize stem borer, *C. partellus*, eggs and early instars on maize due to rainfall. The reduction was significant for larvae located inside leaf whorls, but not for larvae inside stems. Nuessly et al. (1991) observed a maximum of 75% dislodgement of *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) eggs on cotton plants after a thunderstorm. They also reported the maximum dislodgement occurred when eggs were located on top of the plant, and less when eggs were located lower on the plant. Sugarcane borer females prefer to oviposit on young leaves, which are the upper most leaves in the canopy (Dale 1994). In the flooded rice system, the survival of dislodged eggs is probably even lower.

The number of injured tillers was lower at 3rd tiller (26.7 ± 10.9 m^{-2}) than at panicle differentiation (47.7 ± 12.3 m^{-2}) or heading (44.6 ± 10.2 m^{-2}). Fewer stem-injured tillers also were observed at harvest when injury occurred at 3rd tiller (11.1 ± 7.2 m^{-2}) than at panicle differentiation (21.4 ± 10.6 m^{-2}) or heading (25.1 ± 8.7 m^{-2}). Stem

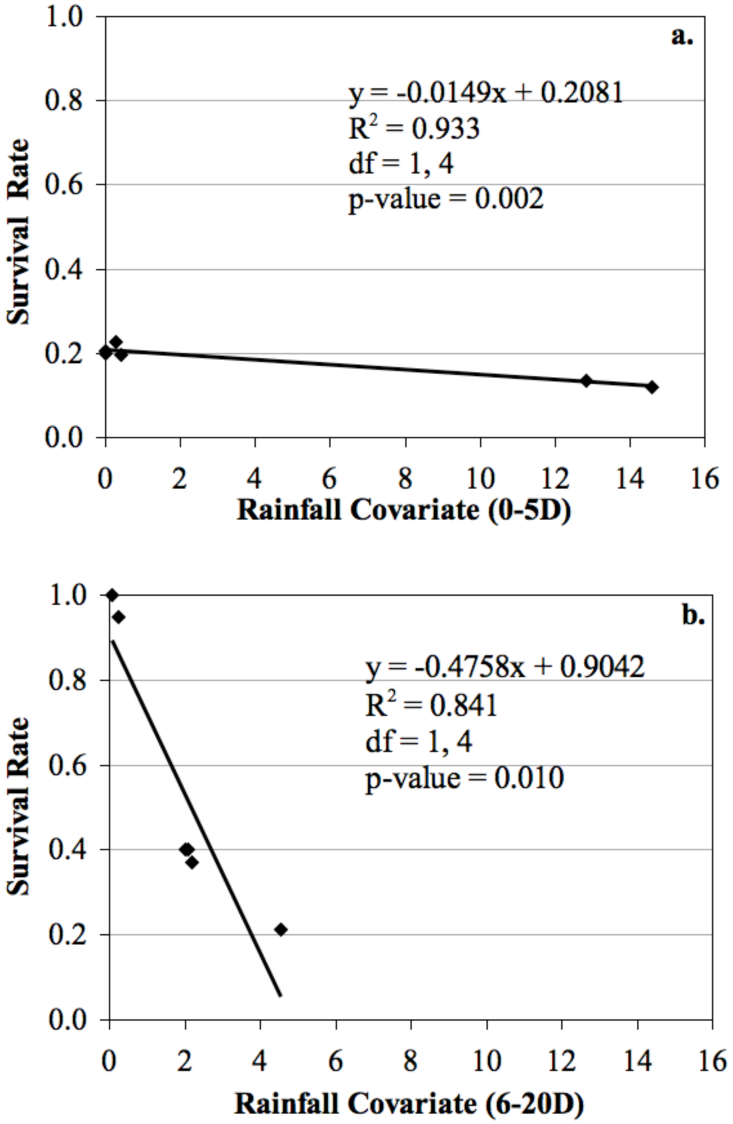


Fig. 2.1. The impact of rainfall on sugarcane borer survival when injury occurred during panicle differentiation and heading for a) survival to the end of the 1st instar and b) survival from the end of the 1st instar to the early 3rd instar.

Injury during early vegetative stages can result in dead heart tillers, which die before harvest (Pathak and Patanakamjorn 1971, Chaudhary et al. 1984). As a result, the number of stem-injured tillers at harvest very likely underestimated the total number of stems injured during this stage. To correct for this bias, the number of stem-injured tillers (i_s) was approximated by the number of stem-injured tillers at harvest (i_h) divided by the proportion which survived to harvest (s), with the constraint that the estimates can not be greater than the number of injured tillers (I), including background injury (b). (Eq. 2.3).

$$i_s = \begin{cases} i_h/s & \text{if} \quad (i_h/s) < (I+b) \\ I+b & \text{if} \quad (i_h/s) \geq (I+b) \geq i_h \\ i_h & \text{else} \end{cases} \tag{2.3}$$

Survival of stems that were injured during the 3rd leaf stage were derived for Cocodrie (47.3%), Francis (67.9%), and Jefferson (57.2%), estimated as the number of dead heart tillers divided by the number of stem-injured tillers, obtained from a biological control study adjacent to the present study during 2005 and 2006 (Lv et al. unpublished data). The corrected estimates for the number of stem-injured tillers at 3rd tiller were 37.0 m^{-2} (2004), 6.7 m^{-2} (2005), and 8.8 m^{-2} (2006), and the proportion of injured tillers with stem injury was 0.95 (2004), 0.17 (2005), and 0.79 (2006). When injury occurred during the two latter stages, ca. 100% of stem-injured tillers survived to harvest; however, in some cases injury resulted in partial or complete panicle death.

Egg density explained 67.4% of the variability in the number of injured tillers, 21.9% of the variability in the number of stem-injured tillers, and 15.1% of the variability in the number of stem-injured tillers that survived to harvest. The number of injured tillers increased with increasing egg density. In contrast, the number of stem-injured tillers and the number of stem-injured tillers that survived to harvest only increased up to "Density 2" (Fig. 2.2a). The significant year × density interaction on this variable was due to stem-injured tillers increasing greatly at higher release densities in 2004, but not in 2005 and 2006 (Fig. 2.2b). Regression of the number of injured tillers against egg density provided significant linear and quadratic terms (Table 2.3), with injury increasing asymptotically with egg density. Regressions of the number of stem-injured tillers that survived to harvest against egg density provided significant linear terms for 2004 to 2006, and a significant quadratic term for 2004.

Cultivar, although statistically significant, only explained 0.2% and 2.1% of the variability in the number of injured tillers and the number of stem-injured tillers, respectively. Although morphological differences exist, all three of the cultivars used in our study were derived from southeast U.S. rice germplasm having relatively similar pedigrees. The results suggest it might be necessary to pursue wider crosses to incorporate traits with high levels of resistance to stem borers. Pathak (1969) estimated the resistance of 10,000 rice cultivars and reported 20 show high non-preference and/or antibiosis to striped stem borer. Pathak also reported hybrid cultivars derived from resistant cultivars showed higher levels of resistance to striped stem borer than either parent.

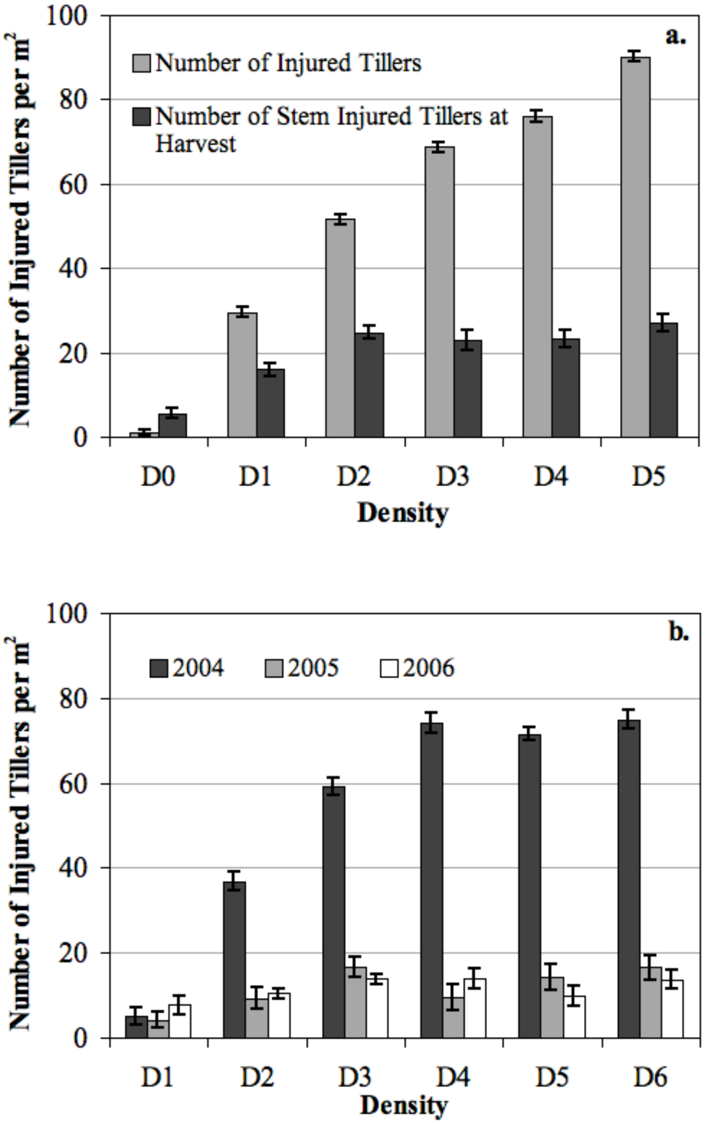


Fig. 2.2. The impact of density on sugarcane borer injury ($\bar{x} \pm 1/2$ *C.I.*) for a) number of injured tillers and stem-injured tillers at harvest averaged across years, and b) number of stem-injured tillers at harvest for each year.

Table 2.3. Polynomial regression of sugarcane borer injury as a function of initial sugarcane borer density

Year	r^2	Intercept	P > t	Density	P > t	Density^2	P > t
			Number of Injured Tillers 10-12 Days after Infestation				
2004-2006	0.51	1.10	0.379	0.16	~ 0	-1.85E-04	~ 0
			Number of Stem-injured tillers at Harvest				
2004	0.40	1.59	0.157	0.10	~ 0	-1.56E-04	~ 0
2005	0.07	1.39	0.035	0.02	0.049	-2.34E-05	0.265
2006	0.03	1.88	~ 0	0.01	0.138	-1.20E-05	0.367

Impact of Injury on Tillering. Tiller density was significantly affected by year, stage, cultivar, density, and the year × stage, year × cultivar, year × density, and year × stage × cultivar interactions (Table 2.2). Mean tiller density was significantly higher in 2004 (326.9 ± 72.8 tillers m^{-2}) and 2005 (334.0 ± 53.3 tillers m^{-2}) than in 2006 (287.0 ± 45.3 tillers m^{-2}). Stepwise regressions showed tiller density was affected by the degree-days (*DD*) from planting to when injury occurred, and the proportion of stem-injured tillers (p_s) at 3rd tiller and heading, and was affected by the same factors and the proportion of injured tillers (p_i) when injury occurred at panicle differentiation (Eqs. 2.4a-c).

$$\begin{aligned} T_{3T} &= 0.828 + 0.0000421DD - 1.05p_s - 0.000000190DD^2 \\ &(R^2 = 0.47, df = 6, 47, p < 0.0001) \end{aligned} \tag{2.4a}$$

$$\begin{aligned} T_{PD} &= -0.806 + 0.00341DD + 0.230p_i + 1.81p_s - 0.00000151DD^2 \\ &-1.59p_i^2 - 0.00312DDp_s + 3.45p_ip_s \\ &(R^2 = 0.82, df = 7, 46, p < 0.0001) \end{aligned} \tag{2.4b}$$

$$\begin{aligned} T_H &= -3.37 + 0.00610DD - 1.44p_s - 0.00000210DD^2 + 2.08p_s^2 \\ &\quad (R^2 = 0.60, df = 4, 49, p < 0.0001) \end{aligned} \tag{2.4c}$$

where:

T_{3T} = Normalized rice tiller density when injury occurred at 3rd tiller

T_{PD} = Normalized rice tiller density when injury occurred at panicle differentiation

T_H = Normalized rice tiller density when injury occurred at heading

Figure 2.3 shows contour plots for normalized mean tiller density as a function of proportion of injured tiller and proportion of stem-injured tiller for each stage. Compensation is detectable following injury when normalized tiller density is equal to or greater than 1. Compensation during 3rd tiller and panicle differentiation, was observed when both the proportion of injured tillers and the proportion of stem-injured tillers were at low levels. Rice compensated for up to 20% of tiller injury and 8% of stem injury at 3rd tiller. In contrast, rice compensated for up to 36% of tiller injury and 17% of stem injury at panicle differentiation. During heading, compensation was observed for up to 48% of tiller injury and up to 16% of stem injury.

Analysis of variances for individually sampled plants in 2004 showed the effect of the plant injury category on number of tillers for both injured and uninjured plants (Table 2.4). The number of tillers per injured plant (3.59 ± 0.84 tillers) was greater than for uninjured plants (3.25 ± 1.08 tillers). Analysis of variances using 2005 and 2006

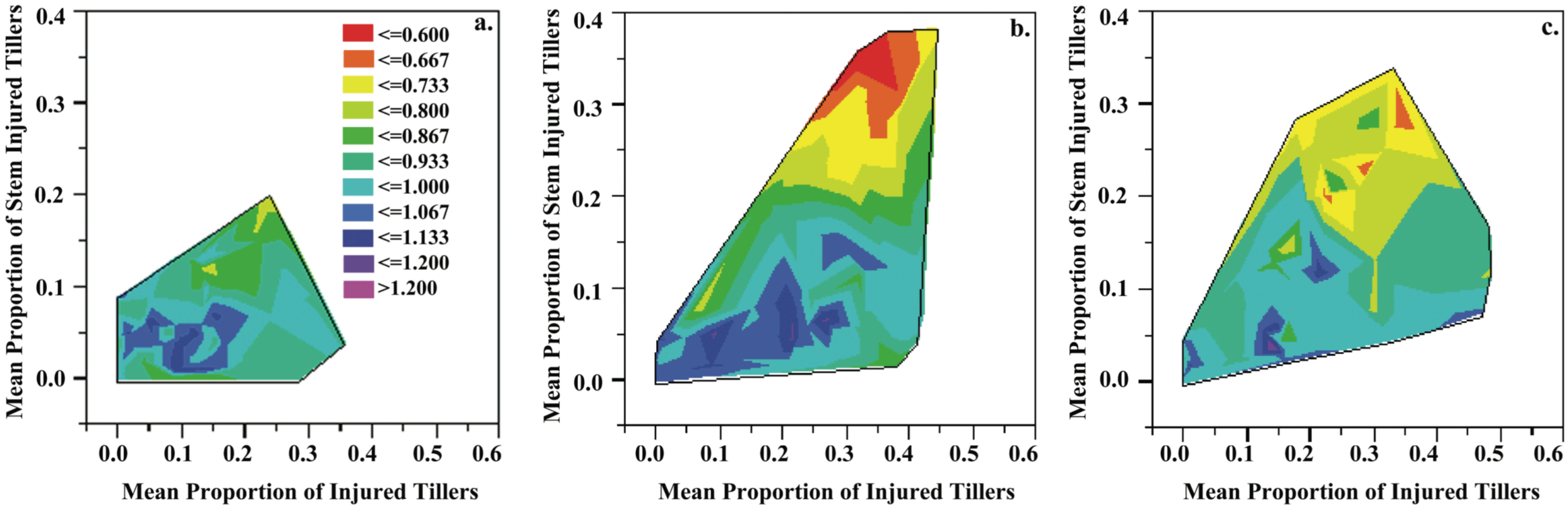


Fig. 2.3. Contour plots of normalized mean tiller density as a function of tiller and stem injury for a) 3rd tiller, b) panicle differentiation, and c) heading.

Table 2.4. ANOVAs of number of tillers per plant, and grain yield per tiller

Source of Variances	Number of Tillers per Plant			Grain Yield per Tiller		
	df	F	P > F	df	F	P > F
			ANOVA of 2004 Data			
Stage	2	0.9	0.460	2	0.1	0.909
Error (1)	6			6		
PC[a]	1	5.1	0.025	1	~ 0	0.989
Stage × PC	2	1.6	0.205	2	22.3	0.002
Error (2)	176			6		
TC(PC)	-	-	-	1	4.1	0.045
Stage × TC(PC)	-	-	-	2	5.0	0.008
Error (3)	-	-	-	243		
			ANOVA of 2005-2006 Data			
Year	1	15.6	0.002	1	5.0	0.045
Stage	2	5.6	0.019	2	1.2	0.333
Year × Stage	2	0.9	0.437	2	0.1	0.885
Error (1)	12			12		
Cultivar	2	14.6	~ 0	2	5.6	0.011
Year × Cultivar	2	1.2	0.331	2	5.6	0.010
Stage × Cultivar	4	0.4	0.843	4	1.2	0.353
Year × Stage × Cultivar	4	2.5	0.073	4	3.2	0.033
Error (2)	23			23		
PC	2	9.3	~ 0	2	2.1	0.126
Year × PC	4	0.7	0.627	2	~ 0	0.974
Stage × PC	2	1.1	0.341	4	1.1	0.380
Cultivar × PC	4	0.7	0.602	4	0.8	0.539
Year × Stage × PC	4	0.9	0.471	4	0.7	0.604
Year × Cultivar × PC	8	0.7	0.733	4	2.3	0.060
Stage × Cultivar × PC	4	1.2	0.324	8	1.6	0.121
Year × Stage × Cultivar × PC	7	0.6	0.735	7	2.0	0.047
Error (3)	910			892		
TC(PC)	-	-	-	3	23.6	~ 0
Year × TC(PC)	-	-	-	3	2.4	0.068
Stage × TC(PC)	-	-	-	6	2.0	0.049
Cultivar × TC(PC)	-	-	-	6	2.2	0.038
Year × Stage × TC(PC)	-	-	-	5	1.7	0.128
Year × Cultivar × TC(PC)	-	-	-	6	0.9	0.513
Stage × Cultivar × TC(PC)	-	-	-	10	1.2	0.283
Year × Stage × Cultivar × TC(PC)	-	-	-	7	1.7	0.103
Error (4)				2218		

[a] PC refers to the plant injury category

[b] TC(PC) refers to the tiller injury category nested within the plant injury category

individual plant data showed the number of tillers per plant was significantly affected by year, cultivar, crop growth stage, and plant injury category. The mean number of tillers per plant in 2005 (3.51 ± 1.49 tillers) was greater than in 2006 (3.04 ± 1.23 tillers). Cocodrie had the greatest number of tillers per plant (3.68 ± 1.49 tillers), followed by Jefferson (3.36 ± 1.42 tillers) and Francis (2.82 ± 1.06 tillers). The mean number of tillers per plant was 3.22 ± 1.35, 3.40 ± 1.46, and 3.24 ± 1.34 when injury occurred at 3rd tiller, panicle differentiation, and heading, respectively. Although a significant stage effect was observed with the ANOVA, multiple comparisons failed to detect a difference between the three crop growth stages.

The mean tiller number for leaf and leaf sheath injured plants (3.52 ± 1.37) and stem injured plants (3.80 ± 1.60) was significantly greater than the mean for uninjured plants (3.11 ± 1.30). The difference in tiller density comparing injured and uninjured plants was not a result of larval selection, because observations of the location of injured tillers indicated larvae disperse randomly from egg masses.

Akinsola (1984) reported rice tillers injured by *Sesamia botanephaga* Tams and Bowden (Lepidoptera: Noctuidae) at vegetative and reproductive stages produce additional tillers. Islam and Karim (1999) reported that although compensatory tillers produce lighter panicles, plants can fully compensate for up to 20% of dead heart tillers when injury occurs during vegetative stages. They also reported rice compensates for stem borer injury by converting unproductive tillers to productive tillers, and producing tillers from aerial nodes when injury occurs during reproductive stages (Islam and Karim 1997). Jiang and Cheng (2003) reported rice plants infested with striped stem borer produce ca. one tiller more than control plants two weeks after infestation when the fertilization rate is 13.0 to 26.0 g N m^{-2}. Significant compensation was not observed when the fertilization rate was not within this range. In the present study, the fertilization rate was 22.4 g N m^{-2}, and rice plants with stem injury produced ca. 0.69 more tiller than uninjured plants, corresponding to 22% more tillers per plant.

Plant density was higher in the present study (111.1 plants m^{-2}) than for research discussed in the previous paragraph (26.7-51.3 plants m^{-2}), which used potted plants or was conducted in low-density hill production systems. Therefore, competition between adjacent plants was expected to be higher in this study. Chi-square analyses failed to detect a significant effect of injury on the number of tillers on adjacent uninjured plants ($p = 0.563$ for Cocodrie, $p = 0.071$ for Francis, and $p = 0.540$ for Jefferson). The lack of detectible between-plant compensation suggests competition between adjacent plants was not significantly reduced by injury. A putative mechanism for compensation is the relocation of photosynthate and nitrogen of injured tillers, which stimulated the initiation and development of other tillers within the same plant. Gupta et al. (1988) reported carbohydrates from a mother plant and its 1st and 2nd tillers can be translocated between each other. Mimoto et al. (1990) observed translocation of root-absorbed nitrogen between rice tillers. Rubia et al. (1996) indicated translocation of assimilates and nitrogen between tillers occurs during the whole rice season; however, translocation is more active during early crop growth stages.

Impact of Injury on Tiller Yield. Mean grain yield per uninjured tiller was significantly affected by year, stage, cultivar, density, and the year × stage, year ×

cultivar, and year × density interactions. Mean grain yield per injured tiller was significantly affected by year, cultivar, density, and the year × cultivar and stage × cultivar interactions. For both analyses, year explained the greatest variability (Table 2.2). Grain yield per tiller was the greatest in 2004 (2.59 ± 0.48 g/uninjured tiller, 1.61 ± 0.64 g/injured tiller), followed by 2006 (2.29 ± 0.31 g/uninjured tiller, 1.43 ± 0.91 g/injured tiller), and 2005 (1.87 ± 0.30 g/uninjured tiller, 0.85 ± 0.91 g/injured tiller). Grain yield of stem-injured tillers was reduced by 37.7%, 54.1%, and 37.4% in 2004, 2005, and 2006, respectively. The yield reduction for Francis (43.4%) was less than that for Cocodrie (69.5%) and Jefferson (67.1%). For Cocodrie and Jefferson, the mean yield of stem-injured tillers was the lowest when infested at 3rd tiller (0.63 ± 0.88 g for Cocodrie, 0.74 ± 0.77 g for Jefferson), followed by panicle differentiation (1.16 ± 0.90 g for Cocodrie, 1.13 ± 0.86 g for Jefferson) and heading (1.59 ± 0.71 g for Cocodrie, 1.72 ± 0.69 g for Jefferson). For Francis, the mean yield of stem-injured tillers was the lowest when infested at 3rd tiller (1.36 ± 0.92 g), followed by heading (1.62 ± 0.86 g) and panicle differentiation (2.01 ± 1.06 g). When infested in the two latter stages, yield loss was greater at panicle differentiation for Cocodrie and Jefferson and less for Francis. Pathak and Patanakamjorn (1971) reported the capacity for tolerance and compensation at different crop growth stages may differ with cultivar. In the present study, mean yield per tiller was not a function of the degree-days when injury occurred, the proportion of injured tillers, or the proportion of stem-injured tillers at each crop stage.

Analysis of variances for individually sampled tillers (2004) showed the yield per tiller was significantly affected by the tiller injury, the stage × plant injury interaction, and the stage × tiller injury interaction (Table 2.4). Averaged across stages of crop growth, grain yield per uninjured tiller either for an uninjured plant (2.21 ± 0.59 g tiller^{-1}) or an injured plant (2.35 ± 0.83 g tiller^{-1}) was greater than grain yield per injured tiller (2.08 ± 1.09 g tiller^{-1}). However, when infestation occurred during panicle differentiation, grain yield of injured tillers (2.49 ± 1.00 g tiller^{-1}) was greater than for uninjured tillers in injured plants (2.20 ± 0.82 g tiller^{-1}) and uninjured tillers in uninjured plants (2.11 ± 0.71 g tiller^{-1}) (Fig. 2.4a), suggesting the occurrence of a compensatory response. Although significance was observed in the ANOVA, significant differences were not observed with the multiple comparison tests.

Analysis of variances using 2005 and 2006 individually sampled tillers showed grain yield per tiller was affected by year, cultivar, and the year × cultivar, stage × tiller injury category, and year × cultivar × stage interactions. The mean grain yield per tiller was lower in 2005 (1.90 ± 0.02 g tiller^{-1}) than in 2006 (2.13 ± 0.02 g tiller^{-1}). Francis produced the largest panicles (2.15 ± 0.02 g tiller^{-1}), followed by Cocodrie (1.95 ± 0.03 gtiller^{-1}) and Jefferson (1.95 ± 0.03 g tiller^{-1}). Mean yield of leaf and leaf sheath injured tillers for the three crop growth stages was 2.46 ± 0.23 g, 2.15 ± 0.11 g, and 1.94 ± 0.12 g on leaf and leaf sheath injured plants, and 2.86 ± 0.12 g, 2.48 ± 0.17 g, and 2.03 ± 0.17 g on stem injured plants. Leaf and leaf sheath injured tillers produced larger panicles than uninjured tillers (2.05 ± 0.02 g) when injury occurred at the two earlier crop growth stages, further suggesting the presence of compensation (Fig. 2.4b).

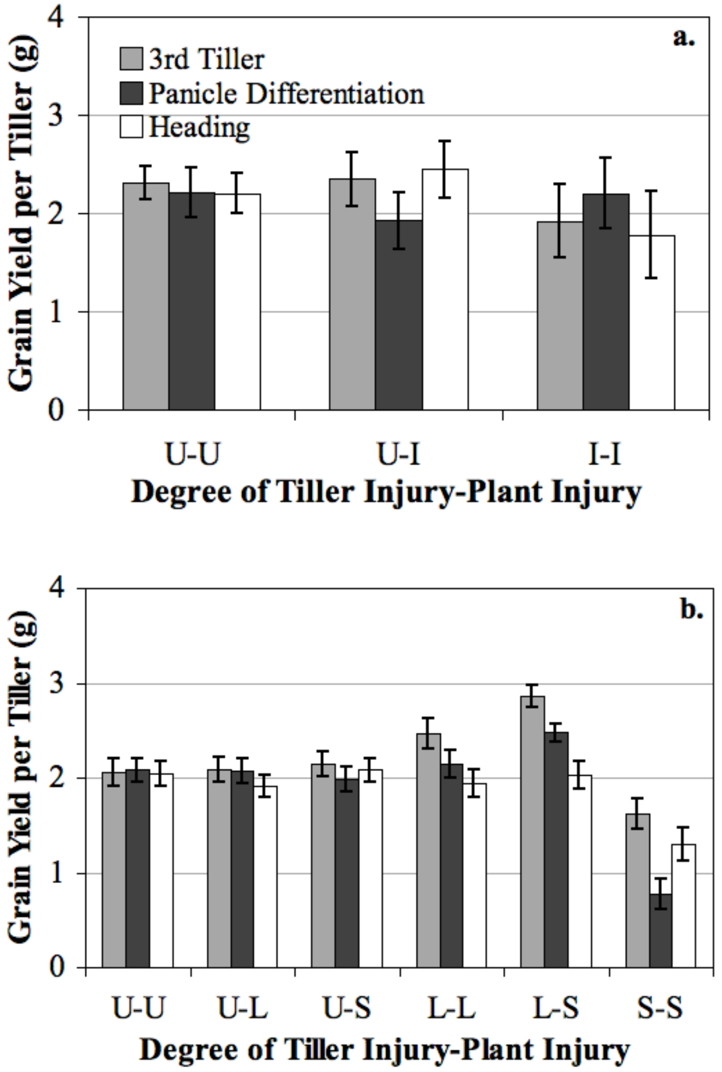


Fig. 2.4. The impact of stage, cultivar, and injury on grain yield per tiller ($\bar{x} \pm 1/2$ *C.I.*) for a) Francis for 2004 and b) all cultivars combined for 2005-2006 (U-uninjured, L-leaf and leaf sheath injured, S-stem injured).

Rubia et al. (1996) tracked the assimilation of CO_2 and the allocation of photosynthate in leaf-injured rice plants using $^{14}CO_2$ and reported the photosynthesis rate of uninjured leaves on injured tillers was greater than that of uninjured leaves on uninjured tillers. Three putative mechanisms for elevated photosynthesis are: 1) assimilation demand by the sink organs that were previously supported by the injured leaves stimulates photosynthesis in the remaining leaves, 2) partial defoliation allows an improved supply of cytokinins to the remaining leaves, and results in an increase concentration of carboxylation enzymes, and 3) nitrogen is translocated from injured leaves to uninjured leaves, which increases the nitrogen concentration and photosynthesis rate of uninjured leaves.

Impact of Injury on Unit Area Yield. Unit area yield integrates the effect of injury on both tiller density and yield per tiller. Grain yield was significantly affected by year, stage, cultivar, density, and the year × stage, year × cultivar, year × density, and year × stage × cultivar interactions (Table 2.2). The greatest yield was observed in 2004 (700.2 ± 153.1 g m^{-2}), followed by 2006 (626.6 ± 113.0 g m^{-2}) and 2005 (602.4 ± 96.9 g m^{-2}). Stepwise regressions showed yield was affected by the degree-days from planting to when injury occurred (DD) and the proportion of stem-injured tillers (p_s) when injury occurred at either 3rd tiller or heading, and was affected by the same factors and the proportion of injured tillers (p_i) when injury occurred at panicle differentiation (Eqs. 2.5a-c).

$$\begin{aligned} Y_{3T} &= -5.13 + 0.0191DD - 7.94p_s - 0.0000150DD^2 + 0.0137DDp_s - 1.51p_s^2 \\ &(R^2 = 0.43, df = 5, 48, p < 0.0001) \end{aligned} \tag{2.5a}$$

$$Y_{PD} = -0.581 + 0.00290DD - 0.260p_i + 1.77p_s - 0.00000137DD^2 - 0.00203DDp_s \quad (R^2 = 0.70, df = 5,48, p < 0.0001) \tag{2.5b}$$

$$Y_H = -3.05 + 0.00570DD - 1.59p_s - 0.00000192DD^2 + 2.48p_s^2 \quad (R^2 = 0.60, df = 4,49, p < 0.0001) \tag{2.5c}$$

where:

Y_{3T} = Normalized yield when injury occurred at 3rd tiller

Y_{PD} = Normalized yield when injury occurred at panicle differentiation

Y_H = Normalized yield when injury occurred at heading

Figure 2.5 shows contour plots for normalized mean grain yield per m^2 as a function of the proportion of injured tillers and the proportion of stem-injured tillers for each stage. Rice compensated for up to 23% of tiller injury and 10% of stem injury at 3rd tiller, 42% of tiller injury and 17% of stem injury at panicle differentiation, and 28% of tiller injury and 14% of stem injury at heading. When injury occurred at 3rd tiller, compensation was the greatest when ca. 5.0% of stems were injured. When injury occurred at panicle differentiation, compensation was the greatest when 2.0% of stems were injured. When injury occurred at heading, compensation was the greatest when1.8% of stems were injured. When injury occurred during 3rd tiller and heading, compensation was due entirely to increased tiller density, with panicle size not significantly affected. When injury occurred during panicle differentiation, 89.2% and 10.5% of the compensation was due to an increase in the number of reproductive tillers

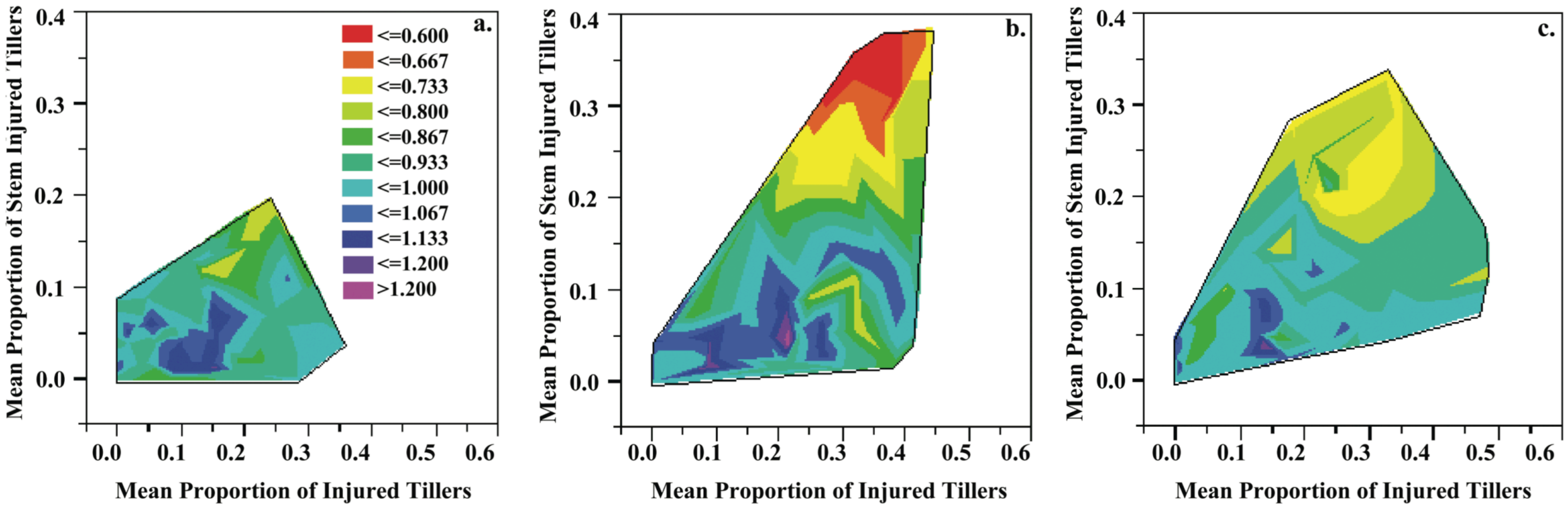


Fig. 2.5. Contour plots of normalized mean yield m^{-2} as a function of tiller and stem injury for a) 3rd tiller, b) panicle differentiation, and c) heading.

and an increase in panicle size, respectively. Economic thresholds for the sugarcane borer on rice are not available for either Texas or Louisiana (Way and Espino 2008, Ring et al. 2006). Rice is usually treated for the sugarcane borer when signs of field infestation (dead hearts or whiteheads) are observed (Ring et al. 2006). The results suggest rice can often compensate for relatively high levels of injury.

Conclusions

The present study evaluated injury by the sugarcane borer to rice and the compensatory response of rice to injury. Injury was affected by the crop growth stage when injury occurred. Less injury was observed when rice was infested at the third tiller stage due to the lower survival of 1st instars. When injury occurred during the two latter infestations, injury was negatively correlated with rainfall, which resulted in the dislodgement and mortality of eggs and larvae. Two mechanisms of tolerance and compensation were observed. Rice tillers can compensate for relatively high levels of stem injury by producing additional reproductive tillers, and for leaf and leaf sheath injury by producing larger panicles.

CHAPTER III

FIELD EVALUATION AND THEORETICAL ANALYSIS OF THE IMPACT OF *COTESIA FLAVIPES* (HYMENOPTERA: BRACONIDAE) AS AN AUGMENTATIVE BIOCONTROL AGENT FOR THE SUGARCANE BORER (LEPIDOPTARA: CRAMBIDAE)

Introduction

Previous research suggests parasitoids can inflict a high level of mortality upon populations of the sugarcane borer, *Diatraea saccharalis* (F.). Browning and Melton (1987) reported *Trichogramma fuentesi* Torre (Hymenoptera: Trichogrammatidae) parasitized 78.7% of sugarcane borer eggs in sugarcane (*Saccharum officinarum* L.) fields in the Lower Rio Grande Valley of Texas. Parra and Zucchi (2004) studied the efficacy of biocontrol on sugarcane in Brazil when using a number of *Trichogramma* species in combination with *Cotesia flavipes* (Cameron), a larval parasitoid, with the highest sugarcane borer population reduction (60.2%) occurring with *Trichogramma galloi* Zucchi and *C. flavipes*. Alam (1980) reported the introduction of *C. flavipes* and *Lixophaga diatraeae* (Townsend) (Diptera: Tachinidae), two larval parasitoids, successfully reduced sugarcane borer injury to sub-economic levels in Barbados. The successful control of the sugarcane borer using *C. flavipes* in sugarcane has also been reported in the Rio Grande Valley of Texas (Meagher et al. 1998).

Trichogramma fuentesi, *T. galloi*, and *L. diatraeae* coevolved with the sugarcane borer, while *C. flavipes* lacks a long-term association with this species. *Cotesia flavipes* is indigenous to the Indo-Australian region, where its hosts are among the *Chilo* genus (Lepidoptera: Crambidae). Studies of *C. flavipes* as a natural enemy of *Chilo* pests in rice were conducted in Japan (Smith et al. 1993) and China (Song et al. 1996, Zhu et al. 1999, You et al. 2000, Li et al. 2005). However, these studies mainly focused on natural control, and did not evaluate the ability of *C. flavipes* to prevent economic loss. While *C. flavipes* is documented to have a major impact on sugarcane borer populations in perennial hosts, such as sugarcane, which are temporally stable, its ability to control stem borer pests on ephemeral host crops, such as rice, is poorly understood. White and Reagan (1999) reviewed previous results from *C. flavipes* releases in the Rio Grande Valley, and concluded this parasitoid was best adapted to control sugarcane borer populations in perennial agriculture systems in subtropical areas, with 3 to 4 years required for introduced parasitoids to reduce and maintain population densities below economic injury levels.

The sugarcane borer has been the predominant stem borer species in rice in both Texas and Louisiana, since shortly following its introduction to Louisiana (Bowling 1967, Williams et al. 1969). The Mexican rice borer, *Eoreuma loftini* (Dyar), was first discovered in Texas in 1980 and now causes yield loss across the Texas ricebelt (Reay-Jones et al. 2005). The occurrence of both the sugarcane borer and the Mexican rice borer has increased in recent years. Way et al. (2006) reported stem borer injury resulted in rice yield losses of up to 60% in Texas. Among all stem borers recovered from their field sampling, ca. 60% were sugarcane borers.

The main objective of the present research is to determine the potential value of *C. flavipes* as an augmentatively released agent for biocontrol of the sugarcane borer on rice. Life table parameters for both the sugarcane borer and *C. flavipes*, obtained from published data and focused experiments presented herein, were incorporated into a simulation model of seasonal population dynamics. A range of overwintering sugarcane borer larval densities and timings and rates of *C. flavipes* release were simulated. A cost/benefit analysis was conducted by combining estimates of yield loss and parasitoid rearing and release costs. A secondary objective is to examine the potential for using *T. galloi* to provide economic control of the sugarcane borer. This species has been well studied and life table parameters governing parasitism have been developed or are available for similar species (Cônsoli and Parra 1996).

Methods and Materials

Field Experiment. A field experiment was conducted in 2005 and 2006 at the Texas A&M AgriLife Research and Extension Center at Beaumont. The soil is a fine montmorillonite and thermic Entic Pelludert (Chen et al. 1989). Fields were planted on April 22, and April 19 in 2005, and 2006, respectively, using a 0.18 m-row spacing.

A randomized complete block split-split plot experimental design was used each year. Each of the three blocks contained three plots, one for each of the three cultivars, Cocodrie, Francis, and Jefferson. Cocodrie and Francis were planted at a rate of 120 kg seed ha^{-1}, while Jefferson was planted at 144 kg seed ha^{-1} to accommodate a lower germination rate. Each plot contained three split plots, each representing a growth stage for infestation. Each split plot was 3.25 m × 6 rows (0.178 m row^{-1}), with 0.25 m at each end as buffers. Each split plot in turn consisted of five split-split plots, each 0.5 m in length. The five split-split plots represented five egg densities (0, 150, 300, 450, 600 eggs m^{-2}). The zero control split-split plot was used to evaluate background borer infestation levels. The control split-split plot was separated from the other split-split plots by a 0.25 m buffer.

Borer injury to rice is affected by cultivar specific phenotypic traits, including plant height, tiller density, and stem diameter (Jodon and Ingram 1948, Israel 1967, Patanakamjorn and Pathak 1967). The cultivars used in this experiment were chosen to represent a range of these phenotypic traits. Cocodrie (Cypress // L-202 / Tebonnet) is moderately tall, produces the highest tiller density, and has the smallest stem diameter. Francis (Lebonnet / Dawn // Starbonnet / Lagrue) is the tallest, produces the fewest tillers, and has a moderate stem diameter. Jefferson (Rosemont // Vista / Lebonnet) is the shortest, produces an intermediate tiller density, and has the largest stem diameter (Lv et al. 2008).

Three crop growth stages were selected, corresponding to third tiller (ca. 40 days after seeding), panicle differentiation (ca. 70 days after seeding), and heading (ca. 100 days after seeding), which also coincide with the first three sugarcane borer larval generations. The three stages represent a period of rapid tiller productive and vegetative growth, a period of transition from vegetative to reproductive development, and a period of rapid grain filling. With the exception of the third tiller stage, which was estimated by visual observation, the timing of each crop stage was estimated using the Rice Development Advisory Program (Wilson et al. 2004), which is a heat driven rice phenology model, with the climatic records during the three rice seasons obtained from the database described in Wilson et al. (2005).

The four non-zero densities were randomly assigned to four adjoining split-split plots by placing sugarcane borer egg masses on the youngest expanded leaves, mimicking adult oviposition preference (Dale 1994). From 1 to 4 of the inner rows of each plot were infested, corresponding to the four non-zero densities, respectively, with only the two inner most rows chosen for the two lowest non-zero densities. Each egg mass, ca. 75 eggs that were darkened and ready to hatch, was attached to a tiller located in the center of a row using a paper clip.

The four non-zero split-split plots were covered with 2.5 m (l) × 1.2 m (w) × 1.25 m (h) polyester screened cages (see *Cage Construction* section) immediately following placement of sugarcane borer egg masses. Each control split-split plot was covered with a 0.85 m (l) × 1.2 m (w) × 1.25 m (h) cage, to prevent infestation by released sugarcane borers. In 2005, 20 newly emerged *C. flavipes* females and 5 newly emerged males were released into each cage covering non-zero split-split plots, 15 days after sugarcane borer release. The female/male sex ratio used in each release mimicked the average sex ratio (4:1) of the Beaumont *C. flavipes* colony (Lv personal observation). In 2006, the release rate was increased to 100 females and 25 males per cage to increase the parasitism rate.

Cages were removed three days after parasitoid release. Each split-split plot was divided into 24 subsamples, each 12.5 cm × 1 row. Tillers within each subsample were bundled, labeled, cut at the base, and returned to the lab for processing. For each injured tiller, leaves were peeled from the stem and the stem was slit to check for the presence of larvae. The number of injured tillers and recovered larvae were recorded for each subsample. For the 1st infestation in 2005, instars were determined based on head capsule widths (Roe et al. 1982). Third or later instars, which were considered as suitable hosts for *C. flavipes* (Wiedenmann et al. 1992), were placed on artificial diet and reared in the lab (see *Sugarcane Borer Colony* section) until they either died or pupated, or until parasitoid cocoons were observed. To confirm that *C. flavipes* does not parasitize 1st and 2nd instars, all recovered larvae from the later infestations were reared in the lab. Results showed *C. flavipes* parasitize sugarcane borer larvae of 2nd instar size, but the larval instar might be underestimated because larvae might molt more than once without appreciably increasing in size. As a result of these finding, subsequently recovered larvae were classified as either small (head capsule width < 0.93 mm, ca. 2nd and 3rd instars), medium (0.93 mm ≤ head capsule with < 1.32 mm, ca. 4th instar), or large (head capsule with ≥ 1.32 mm, ca. 5th instar). *Cotesia flavipes* cocoons obtained from parasitized sugarcane borer larvae were placed in 30 ml plastic cups, as used for the *C. flavipes* colony. The number and gender of emerging parasitoids were recorded.

Cage Construction. Field cages were constructed using 0.5 inch dia. (1.27 cm) plastic pipes (CRESLINE HC-SOR11 CPVC 4120-100 PSI), and were screened with 0.25 mm polyester netting (American Home and Habitat Inc. Squires, MO.). The large cages, which covered the infested split-split plots, consisted of four arches (120 cm (w) × 125 cm (h)), four widthwise base-frame members (120 cm), two lengthwise base-frame members (250 cm), and one spine (250 cm) (Fig. 3.1a). The small cages that covered the uninfested control split-split plots consisted of two arches (120 cm (w) × 125 cm (h)), two widthwise base-frame members (120 cm), two lengthwise base-frame members (85 cm), and one spine (85 cm) (Fig. 3.1b). Each arch was made from a 300 cm pipe. Two T-joints were used to connect each arch and widthwise base-frame. One 3 cm length pipe was connected to the lower end of each T-joint (Fig. 3.1c), which was in turn connected to each lengthwise base-frame. For each large cage, each lengthwise base-frame was constructed using three 83.3 cm pipes (Fig. 3.1d), connected using two T-joints, with an elbow joint attached to each end. For each small cage, each lengthwise base-frame had an elbow joint attached to each end (Fig. 3.1e). The connections used in each base-frame were glued with PVC cement (Ace 43691). The spine for each large cage was a 250 cm pipe, and the spine for each small cage was an 85 cm pipe. For each cage, the spine went across the top of each arch, and was bound to them at each intersection with zip ties.

Netting was sewn using a Singer 5050 sewing machine. For each large cage, two pieces of 260 cm (l) × 170 cm (w) netting, each representing a side of the cage, were sewn together along the lengths, with the seam running lengthwise along the top of the cage. Arc-shaped netting, 130 cm (w) × 135 cm (h), was sewn to create each end of each cage. The netting was connected to the cage frame using 3 cm × 5 cm loops made from the netting material. The loops were sewn to the inside of the netting ca. 10 cm above the

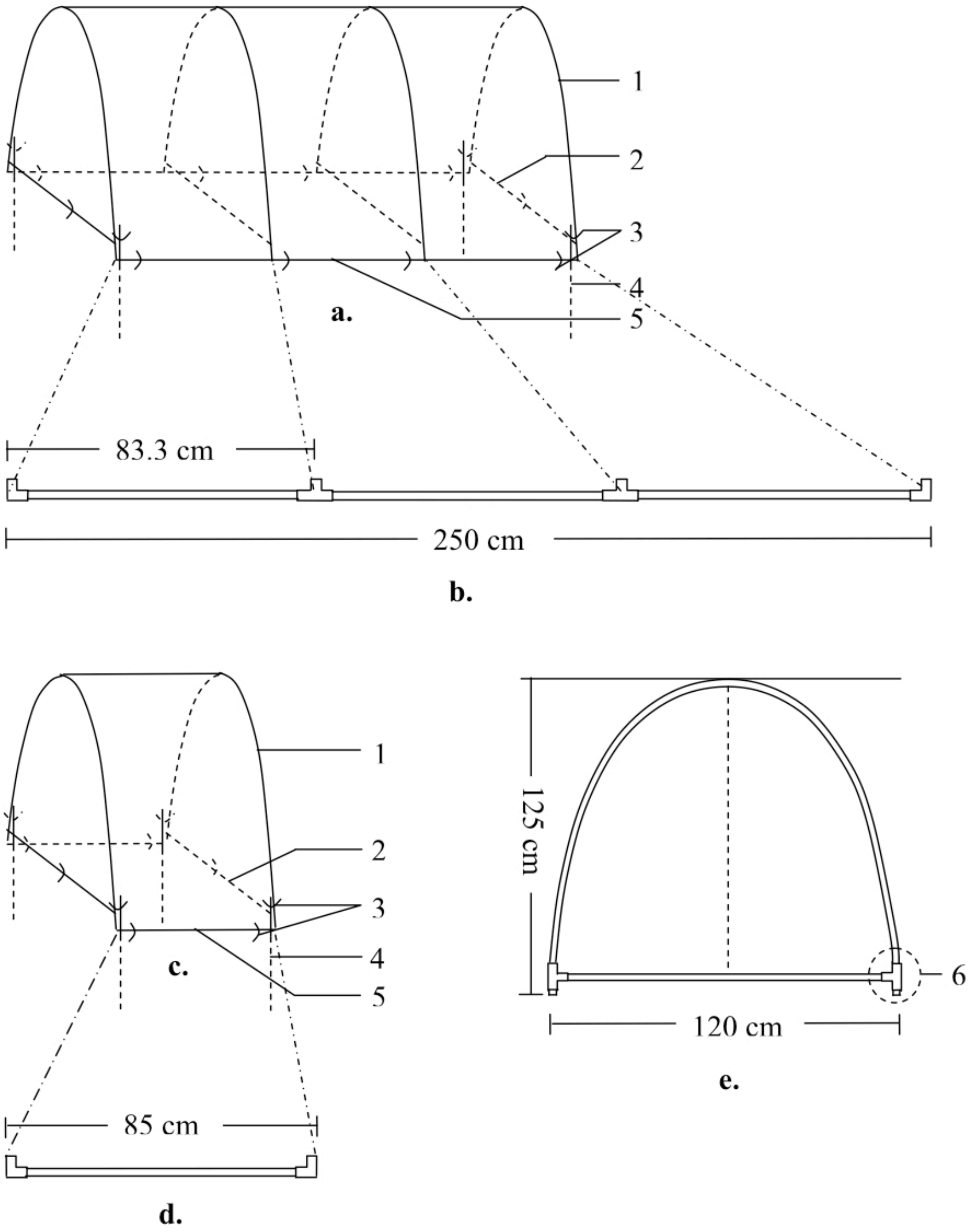


Fig. 3.1. Field cage design. a) large cage, b) lengthwise base-frame member of large cage, c) small cage, d) lengthwise base-frame member of small cage, and e) arch and widthwise base-frame members. 1) arch, 2) widthwise base-frame member, 3) zip tie location, 4) stabilizing pipes, 5) lengthwise base-frame member, and 6) T-joints connecting the arch, widthwise base-frame member, and 3-cm length connector.

bottom edge, and zip ties were inserted into each loop to bind the netting to the base of the frame. For each large cage, 10 loops were sewn, with 4 on each side connecting to the lengthwise base-frame member and 1 at each end connecting to the widthwise base-frame member. For each small cage, 6 loops were sewn, with 2 on each side connecting to the lengthwise base-frame member and 1 at each end connecting to the widthwise base-frame member.

Four 40 cm pipes were used to stabilize each corner of a cage. A 0.5 cm diameter hole was drilled into each pipe ca. 5 cm from one end. Each pipe was placed in the inside corner of a cage and hammered into the ground to a depth of ca. 32 cm, with the drilled hole remaining ca. 3 cm above ground level. A zip tie was inserted through each hole and tied to the bottom of a pipe arch. In a flooded rice field, at least 5 cm of the netting was under water, which prevented *C. flavipes* from escaping under the cage.

Lab Experiment. A lab experiment was conducted at the Texas A&M AgriLife Research and Extension Center at Beaumont to determine the effect of temperature on the maximum number of hosts parasitized per female. The experiment was conducted at 4 temperatures: 22, 25, 28, and 31 ˚C. For each temperature, 10 Petri dishes (ca. 10 cm dia.) were prepared, each containing a thin layer (ca. 0.5 cm) of sugarcane borer diet (see *Sugarcane Borer Colony* section). Seven 3rd instar sugarcane borers and a pair of newly emerged *C. flavipes* adults were placed in each Petri dish. The number of larvae provided to each female exceeds the observed maximum number of hosts parasitized per female by a factor of 3.5 fold (Lv personal observation). The Petri dishes were placed in a Conviron 124 L incubator and maintained at a 14:10 photophase until the parasitoids died. When the *C. flavipes* adults had all died, the larvae were moved to 30 ml diet cups, and reared separately until they either died, pupated, or *C. flavipes* cocoons were observed. The number of dead and parasitized larvae was recorded.

Sugarcane Borer Colony. The sugarcane borers used in the present study were obtained from a Beaumont colony, established using adult sugarcane borer moths reared from eggs obtained from a USDA-ARS colony maintained by Dr. William White, in Houma, LA. The USDA colony has been maintained in the lab since 1989, with wild moths introduced in 2000 and 2006 from a sugarcane field in Houma. The Beaumont colony, including all life stages, was reared in a Conviron 124 L incubator, at 28 ± 1 ˚C and a 14:10 photophase. Each week, an oviposition container was established, using a 1.9 L paper carton. The carton had a 0.5 cm layer of wet vermiculite in the bottom to maintain humidity and was lined with wax paper, which served as an oviposition substrate. A petri dish (10 cm dia.) was placed in the carton to hold ca. 15 female and 15 male pupae. This prevented the pupae from being in direct contact with the wet vermiculite. A 30 ml plastic cup was added to each carton, and contained a cotton ball soaked with 15 ml of 5% sugar water serving as food for the adults. Wax paper was removed and replaced daily, and eggs were collected. This process continued until all the adults had died. Cartons were cleaned using 70% ethanol and reused. Eggs were hatched in plastic bags filled with air and saturated with moisture. Larvae were reared in 30 ml plastic cups (Bio-Serv. Inc., NJ.) containing 15 ml of a soybean flour wheat germ diet produced by Southland Products, Inc., modified from the diet described by Hensley and Hammond (1968).

***Cotesia flavipes* Colony.** A *C. flavipes* colony was established using adults reared from cocoons obtained from a USDA-ARS colony maintained by Dr. William White, in Houma, LA. This colony was initiated in 2003 with field collected *C. flavipes* obtained from Weslaco, TX. The Beaumont colony was maintained in a Conviron 124 L incubator as previously described. Every 4 days, parasitoid cocoons obtained from 25 parasitized sugarcane borer larvae were placed in 30 ml plastic cups for adult emergence. Newly emerged *C. flavipes* adults were kept in the cups for half a day. Parasitized larvae were obtained by exposing individual larvae to *C. flavipes* adults. A single larva was placed in a Petri dish (10 cm dia.) containing 5 12-hr old *C. flavipes* adults that had emerged from a parasitized larva. The oviposition process was observed for up to 5 minutes. If parasitization occurred, the larva was immediately removed and placed in a diet cup and reared as described in the sugarcane borer colony section. Another larva was placed in the vial and the process repeated. If parasitization did not occur within 5 minutes, the larva was replaced. If parasitization did not occur for 3 consecutive larvae, the *C. flavipes* adults were replaced. Parasitism was allowed to continue until ca. 30 parasitized larvae were obtained to maintain the colony, with ca. 100 additional parasitized sugarcane borer larvae produced for each infestation. Approximately 80% of parasitized larvae produced *C. flavipes* adults.

Model Structure. The cohort-based age-structured model consists of sugarcane borer and *C. flavipes* submodels. The sugarcane borer population is initiated from overwintering larvae at the time of diapause termination in early spring. Population progression was simulated in rice through the main crop and in the stubble until the next year's spring emergence. Because ratoon crop production represents only a small percent of the total rice production east of Houston (average of 23% for 2001 to 2007 obtained from the database described in Wilson et al. 2006), it was not simulated. The majority of rice fields in the southern U.S. have stubble that remains in the fields until the next spring. Rice is rarely replanted in the same field two years in a row. Simulation of overwintering larvae provides estimates of the timing of larval diapause termination and subsequent pupal development, and adult emergence the following spring. The immigration and emigration of sugarcane borer moths was assumed to be equal throughout each year. *Cotesia flavipes* population progression was simulated from augmentative release to the last generation each year. White et al. (2004) reported the spring emergence of *C. flavipes* occurs earlier than its host species in temperate and sub-tropical areas. As a result, the 1st generation *C. flavipes* was not simulated due to the adults failing to find suitable hosts for oviposition and failing to produce future generations.

Sugarcane Borer Submodel. The sugarcane borer population was simulated using a physiological time scale (degree-days (DD) > 10.4 ˚C, estimated from King et al. 1975) on a m^2 area basis, with population progression calculated daily. Major differences between the coefficients of developmental variability for each developmental stage (egg, larval, pupal, and adult) required each stage be simulated separately. The mean developmental duration, expressed in DD, of the j^{th} developmental stage ($D_{\tau,j}$ is a function of the daily average temperature (Eq. 3.1). The parameters for the egg, pupal, and adult stages were based on lab developmental duration estimates from King et al.

(1975), while parameters for the larval stage were estimated based on lab data from King et al. (1975), but scaled to the field developmental rate presented herein.

$$D_{\tau,j} = \frac{D_{\tau,j,\min}}{e^{\beta_{j,1}\left|\left(\frac{\tau}{\tau_{j,\min}}\right)^{\beta_{j,2}}-1\right|}} \tag{3.1}$$

where:

τ = Daily average temperature (˚C)

$D_{\tau,j,min}$ = Minimum developmental duration for the j^{th} sugarcane borers stage, expressed as DD, at temperature τ

$\tau_{j,min}$ = Temperature when the minimum developmental duration was observed for the j^{th} stage

$\beta_{j,1\text{-}2}$ = Empirical constants

Developmental variability was incorporated using a modification to the Plant and Wilson (1986) degree-day based distributed maturation algorithm, allowing development to be incremented on a daily instead of a degree-day basis (Wilson et al. unpublished manuscript). The Plant and Wilson (1986) algorithm divides the life span of the j^{th} stage into n_j age classes, and assumes symmetry in population aging (Eq. 3.2a-b).

$$N_{i,j,k} = N_{i,j,k-1}\varepsilon_j + N_{i-1,j,k-1}\left(1-2\varepsilon_j\right) + N_{i-2,j,k-1}\varepsilon_j \tag{3.2a}$$

$$\varepsilon_j = \frac{n_j s^2_{D_{\tau,j}}}{2D^2_{\tau,j}} \text{ and } \varepsilon_j \leq 0.33 \tag{3.2b}$$

where:

$N_{i,j,k}$ = Sugarcane borer density in the i^{th} age class on the j^{th} stage on the k$^{\text{th}}$ day

ε_j = Probability of aging either faster or slower than the mean developmental rate

$s^2_{D_{\tau,j}}$ = Variance of the developmental duration at temperature τ

The Wilson et al. method contains two coefficients ($\beta_{3,j}$, $\beta_{4,j}$) to allow the use of a daily time step (Eq. 3.3a). Each coefficient is a function of the width of each age class (Δa_j), and the daily cumulative DD (Δt) (Eqs. 3.3b-c). When the number of DD that accumulate during a day equals the width of an age class, $\beta_{3,j}$ and $\beta_{4,j}$ both equal 1.0 and Eq. (3a) collapses to the Plant and Wilson (1986) algorithm.

$$N_{i,j,k} = N_{i,j,k-1}\beta_{3,j}\varepsilon_j + N_{i-1,j,k-1}\left(1-\beta_{3,j}\varepsilon_j-\beta_{4,j}\varepsilon_j\right) + N_{i-2,j,k-1}\beta_{4,j}\varepsilon_j \tag{3.3a}$$

$$\beta_{3,j} = \begin{cases} \dfrac{\Delta a_j}{\Delta t} & \mathit{if} \quad \left(\dfrac{\Delta t}{\Delta a_j}\right) > 1 \\ \left(1-\dfrac{\Delta t}{\Delta a_j}\right)\Big/\varepsilon + \left(\dfrac{\Delta t}{\Delta a_j}\right) & \mathit{if} \quad \left(\dfrac{\Delta t}{\Delta a_j}\right) \le 1 \end{cases} \tag{3.3b}$$

$$\beta_{4,j} = \beta_{3,j} - \left(1-\frac{\Delta t}{\Delta a_j}\right)\Big/\varepsilon_j \tag{3.3c}$$

The width of each age class is a function of temperature. In our analyses, the number of age classes was set to make the width of each age class ca. 20 DD, which is ca. equal to the average DD per day during the rice season, for all stages at the temperatures when the minimum developmental durations occur. The daily increment of DD was calculated based on daily maximum and minimum temperature data using the double-sine approximation method (Allen 1976).

Sugarcane borers can enter diapause at the end of the larval stage during the winter in areas with temperate and sub-tropical climates. Diapause can be induced in 2nd and 3rd instar sugarcane borer larvae by decreasing day length (< ca. 12.9 hr) and decreasing temperatures (< ca. 26.9 ˚C) (estimated from Fuchs et al. 1979, Philogène and Hammond 1984). The proportion of 2nd and 3rd instar larvae that were induced to enter diapause was estimated as a function of day length and temperature (Eq. 3.4a), with day length calculated using the method of Keisling (1982). The proportion that was induced each day was estimated using Eq. (3.4b). Larval development during diapause was simulated using the same method as described in Eq. (3.3a). The diapause duration (502.2 DD) was the difference between the mean time larvae were estimated to enter diapause and the mean time larvae terminated diapause, the latter estimated from Rodriguez-del-Bosque et al. (1995). The standard deviation (σ_d) of diapause duration (86.6 DD) was approximated using Eq. (3.4c). Subsequent pupal and adult development is the same as for non-diapausing sugarcane borers.

$$p_d = Min\left(1, Max\left(0, \left(\beta_5 + \beta_6\tau + \beta_7\ell + \beta_8\ell\tau\right)\right)\right) \tag{3.4a}$$

$$p_{d,k} = 1 - \left(1 - p_d\right)^{1/n_d} \tag{3.4b}$$

$$\sigma_d = \sqrt{\sigma_t^{\,2} - \sigma_i^{\,2}} \tag{3.4c}$$

where:

p_d = Proportion of 2nd and 3rd instars induced to enter diapause at the end of larval development

$p_{d,k}$ = Proportion of 2nd and 3rd instars induced during the k^{th} day

ℓ = day length (hr)

n_d = Number of age class that are sensitive to diapause induction

σ_i^2 = Simulated variance of the timing of diapause initiation

σ_t^2 = Simulated variance of the timing of diapause initiation

$\beta_{5\text{-}8}$ = Empirical constants

Intrinsic survivorship ($S_{\tau,i,j,k}$) was estimated as a function of temperature and age using data from King et al. (1975) (Eq. 3.5a), while extrinsic survivorship was estimated as a function of sugarcane borer age, host plant age (Eq. 3.5b), and rainfall (Eq. 3.5c), using data from Lv et al. (2008) and from the present field experiment. The effect of rainfall on survival of latter instars and pupae is thought to be minimal (Bonhof and Overholt 2001) and was not incorporated into the model. The effect of rainfall on adult survival is unknown but is thought to be minor and was not included in the model. Age specific survival for the i^{th} age class, j^{th} stage, on the k^{th} day ($s_{i,j,k}$) was obtained using Eq. (3.5d).

$$S_{\tau,i,j} = \left(\beta_9 e^{\beta_{10}\left|\left(\frac{\tau}{\tau_{s,\max}}\right)^{\beta_{11}} - 1\right|}\right)^{\left(p_{dev,i,j}\right)^{\beta_{12}}} \tag{3.5a}$$

$$S_{h,i,j} = \begin{cases} 1 & egg\ stage \\ \left(\beta_{13} p_{rice}{}^{\beta_{14}\left(1-p_{rice}\right)^{\beta_{15}}}\right)^{\left(p_{dev,i,j} - p_{dev,egg}\right)^{\beta_{16}}} & larval\ stage \\ \left(\beta_{13} p_{rice}{}^{\beta_{14}\left(1-p_{rice}\right)^{\beta_{15}}}\right) & pupal - adult\ stage \end{cases} \tag{3.5b}$$

$$S_{r,i,j,k} = \begin{cases} e^{\beta_{17} r_k p_{dev,i,j}} & egg - 3^{rd}\ instar\ larvae \\ 1 & otherwise \end{cases} \tag{3.5c}$$

$$s_{i,j,k} = \frac{S_{r,i,j,k} S_{\tau,i,j} S_{h,i,j}}{S_{\tau,i-1,j} S_{h,i-1,j}} \tag{3.5d}$$

where:

$\tau_{s,max}$ = Temperature at which the maximum survival was observed (27.3 °C)

$p_{dev,i,j}$ = Proportion of sugarcane borer development completed at the i^{th} age class of the j^{th} stage

$S_{h,i,j}$ = Extrinsic survivorship as affected by host plant age for the i^{th} age class of the j^{th} stage

p_{rice} = Proportion of rice development completed at the time of the infestation

$p_{dev,egg}$ = Proportion of development completed at the end of the egg stage

$S_{r,i,j.k}$ = Extrinsic survivorship as affected by rainfall the i^{th} age class of the j^{th} stage on the k^{th} day

r_k = Rainfall on the k^{th} day (cm)

$\beta_{9\text{-}17}$ = Empirical constants

Cumulative fecundity per female ($F_{c,\tau,i}$) was estimated as a function of temperature and age using data from King et al. (1975) and Bessin and Reagan (1990) (Eqs. 3.6a-b), with age-specific fecundity ($F_{\tau,i}$) estimated using Eq. (3.6c). The female sex ratio is ca. 1:1 (King et al. 1975).

$$F_{c,\tau,i} = F_\tau \left(\frac{i\Delta a}{D_{\tau,adult}} \right)^{\beta_{18}\left(\frac{i\Delta a}{D_{\tau,adult}} \right)^{\beta_{19}}} \tag{3.6a}$$

$$F_\tau = F_{\tau,\max} e^{\beta_{20}\left| \left(\frac{\tau}{\tau_{f,\max}} \right)^{\beta_{21}} - 1 \right|} \tag{3.6b}$$

$$F_{\tau,i} = F_{c,\tau,i} - F_{c,\tau,i-1} \tag{3.6c}$$

where:

F_τ = Number of eggs produced by a female at temperature τ

$D_{\tau,adult}$ = Development duration of the adult stage

$\tau_{f,max}$ = Temperature when the maximum fecundity was observed (24.3 °C)

$F_{\tau,\,max}$ = Maximum fecundity per female, comparing all temperatures

$\beta_{18\text{-}21}$ = Empirical constants

Cotesia flavipes *Submodel. Cotesia flavipes* population development was simulated using the distributed development method described previously. Major differences between the coefficients of developmental variability required that the immature and adult stage be simulated separately. The mean and standard deviation of *C. flavipes* immature developmental duration is 277.4 DD > 10.4˚C and 8.2 DD, respectively, and were estimated using data from Wiedenmann et al. (1992). The mean and standard deviation of adult developmental duration is 69.8 DD > 10.4˚C and 7.3 DD, respectively, and were estimated using data from Potting et al. (1997). The developmental threshold for *C. flavipes* is not available from the literature, and was assumed to be the same as estimated for the sugarcane borer. Data that quantify the effect of temperature on the degree-day requirement for immature and adult development are also not available. As a result, the mean degree-day requirements for these stages were considered to be constants.

Oviposition preference quantifies departure from random host selection, and can be used to estimate herbivore oviposition, parasitism, and predation based on the availability of different hosts species or age/stage classes (Murdoch 1969, Manly et al. 1972, Chesson 1978, Wilson and Gutierrez 1980, Pickett et al. 1989, Murphy et al. 1991, Reay-Jones et al. 2007). Estimates of oviposition preference by *C. flavipes* for each host instar were derived from the estimated number of larvae and parasitized larvae in each instar at the time of peak parasitization (ca. 1 day after release of the adult *C. flavipes,* Potting et al. 1997). The physiological age-class distribution of total and parasitized larvae at the time of parasitism was obtained from the respective age-class distribution at the time of samplings by using a reverse solution of Eq. (3.3a). Oviposition preference of *C. flavipes* for each instar was derived for each crop growth stage in each year, using Eq.

(3.7a). Weighted estimates of the average oviposition preference for each instar across the three crop growth stages and the two years were derived using Eq. (3.7b).

$$\alpha_{m,s,y} = \frac{N_{h,a,m,s,y} / N_{h,m,s,y}}{Max\left(N_{h,a,m,s,y} / N_{h,m,s,y}\right)} \tag{3.7a}$$

$$\alpha_m = \frac{\dfrac{\sum_{y=1}^{2}\sum_{s=1}^{3}\alpha_{m,s,y}N_{h,m,s,y}}{\sum_{y=1}^{2}\sum_{s=1}^{3}N_{h,m,s,y}}}{Max\left(\dfrac{\sum_{y=1}^{2}\sum_{s=1}^{3}\alpha_{m,s,y}N_{h,m,s,y}}{\sum_{y=1}^{2}\sum_{s=1}^{3}N_{h,m,s,y}}\right)} \tag{3.7b}$$

where:

$\alpha_{m,s,y}$ = Oviposition preference for the m^{th} instar when parasitism occurred at the s^{th} crop growth stage and the y^{th} year

$N_{h,a,m,s,y}$ = Number of parasitized sugarcane borer larvae at peak parasitism in the m^{th} instar when parasitism occurred at the s^{th} crop growth stage and the y^{th} year

$N_{h,m,s,y}$ = Number of sugarcane borer larvae at peak parasitism in the m^{th} instar when parasitism occurred at the s^{th} crop growth stage and the y^{th} year

α_m = Average oviposition preference for the m^{th} instar across the three crop growth stages and two years

The density of *C. flavipes* females attacking the i^{th} larval age class ($N_{p,i}$) is a function of the preference shown by the parasitoids for each larval host age class and the available of sugarcane borer larvae in each age class (Eq. 3.8a), while the density of parasitized larvae in each age class was estimated each day using the Frazer-Gilbert functional response equation (Frazer and Gilbert 1976), developed for a single parasitoid species attacking a single host species or stage (Eq. 3.8b-c). The maximum number of hosts parasitized per female (b_τ) and the effective search rate (s) used by the Frazer-Gilbert equation were estimated using data from the lab and field experiments. The effective female fecundity, defined as the number of *C. flavipes* females that emerged from each parasitized host, was estimated using data from the field experiment.

$$N_{p,i} = N_p \frac{\alpha_i N_{h,i}}{\sum_{i=0}^{n-1} \alpha_i N_{h,i}} \tag{3.8a}$$

$$N_{h,a,i} = N_{h,i}\left(1 - e^{\left(-b_\tau N_{p,i} / N_{h,i}\right)\left(1 - e^{-sN_{h,i}/b_\tau}\right)}\right) \tag{3.8b}$$

$$b_\tau = b_{\tau,\max} e^{-\beta_{22} |\tau - \tau_{p.\max}|^{\beta_{23}}} \tag{3.8c}$$

where:

N_p = *C. flavipes* female density

$N_{h,a,i}$ = Density of parasitized i^{th} age class sugarcane borer larvae

$N_{h,i}$ = Density of the i^{th} age class of sugarcane borer larvae

$b_{\tau,max}$ = Maximum number of larvae parasitized per parasitoid per day across all temperatures

$\tau_{p,max}$ = Temperature at which the maximum parasitization occurs

s = Effective search rate (m^2 parasitoid^{-1} day^{-1})

$\beta_{22\text{-}23}$ = Empirical constants

Simulation Analyses. Ten overwintering diapausing sugarcane borer larvae densities were simulated, ranging from 1 to 10 larvae m^{-2}, with the highest density corresponding to the highest previously observed sugarcane borer diapausing larval infestation, which occurred in a study where natural enemies have been eliminated by the use of broad-spectrum insecticides in the U.S. Gulf coast region (Bessin and Reagan 1993). The effect of the timing of *C. flavipes* release was simulated in 10-day increments from 40 days after rice planting in the spring to main crop harvest. For each release date, 11 *C. flavipes* release densities were simulated, ranging from 0 to 10 females m^{-2}. Higher release rates were not simulated, as the cost would exceed the value of the grain yield. Each simulation was continued for 31 years, using 1978 to 2007 climate data obtained from the *iAIMS* database (Wilson et al. 2007), with the first year's climatic data providing an estimate of the timing of initiation of diapause termination for the first year, and the subsequent 30 years providing estimates of sugarcane borer and *C. flavipes* population dynamics, as affected by year to year climatic variability.

For each of the 3 sugarcane borer generations occurring during main crop rice development, the relative yield, expressed as the proportion of the yield in the absence of injury (Y_u), is a function of the simulated density of the sugarcane borer that entered the 3rd instars, herein referred to as simulated generational cumulative damaging larval density, and the degree-days from rice planting to timing when injury occurred (Eq. 3.9a-c, modified from Lv et al. 2008).

$$\begin{aligned}Y_1 = &-5.14 + 0.0191DD_r - 0.00000199\rho_i - 0.0000150DD_r^{\,2} + 0.00000000343DD_r\rho_i \\ &- 0.00000000000199\rho_i^{\,2}\end{aligned} \tag{3.9a}$$

$$\begin{aligned}Y_2 = &-0.581 + 0.00290DD_r + 0.000000418\rho_i - 0.00000137DD_r^{\,2} \\ &- 0.000000000508DD_r\rho_i\end{aligned} \tag{3.9b}$$

$$\begin{aligned}Y_3 = &-3.05 + 0.00570DD_r - 0.000000398\rho_i - 0.00000192DD_r^{\,2} \\ &+ 0.000000000000155\rho_i^{\,2}\end{aligned} \tag{3.9c}$$

where:

Y_i = Relative yield as affected by the i^{th} generation sugarcane borer larvae

DD_r = Degree-days from rice planting to the time when injury occurred

ρ_i = Density (ha^{-1}) of sugarcane borer larvae reaching the 3rd instar

The impact of sugarcane borer injury on rice yield was assumed to be multiplicative across the three generations, and was estimated as the product of yield in the absence of injury and relative yield as affected by each generation (Eq. 3.10). The average yield for the three cultivars used in our experiment in the absence of injury was 6,776.4 kg ha^{-1} (Lv et al., unpublished data). Lv et al. (2008) conducted a field experiment adjacent to the present study, and reported the yield difference across the same three cultivars was statistically significant, but only explained a small percentage

(0.4%) of the total variability introduced by year, cultivar, crop growth stage, pest density, and random variability. As a result, the cultivar effect was not simulated. For each overwintering larval density and each timing and rate of *C. flavipes* release, the yield loss prevented due to the release was estimated as the difference in yield with and without *C. flavipes* release.

$$Y = Y_u \prod_{i=1}^{3} Y_i \tag{3.10}$$

where:

Y = Rice yield (kg ha^{-1}) as affected by three generations of sugarcane borer injury

Economic Value. The economic value of parasitoid release was estimated for each overwintering larval density, each timing and rate of *C. flavipes* release, and each year as the difference between the value of the yield loss prevented by releasing *C. flavipes* and the cost of the control action (Eq. 3.11).

$$E = vY_p - c \tag{3.11}$$

where:

E = Economic value of *C. flavipes* release (\$ ha^{-1})

v = Market value of the crop per unit of product (\$ kg^{-1})

Y_p = Yield loss prevented by *C. flavipes* release (kg ha^{-1})

c = Cost of pest control (\$ ha^{-1})

The estimated cost of a *C. flavipes* release consists of the cost of rearing, shipping, handling, and release. The cost of *C. flavipes* rearing is ca. $100.00 for 10,000 females (ca. 14,000 males + females), including 66.5% for diet (Southland Products, Inc.) and 33.5% for rearing trays and plastic sheet covers (D. G. Hall, personal communication). The estimated shipping cost is $0.28 per 10,000 cocoons (R. V. Dowell personal communication). The cost of aerial-release is $1.00 per 10,000 parasitoids, plus an additional $24.72 per hectare for the aerial application (S. Penn, personal communication). The market value of rough rice is ca. $0.418 per kg (Chicago Board of Trade Jan. 2009 futures price estimated on Aug. 28, 2008).

Statistical Analyses. Sugarcane borer larvae were removed from the field ca. 18 days after infestation. As a result, the complete developmental duration in rice was not available. The developmental duration on rice in the field was estimated as the ratio of the degree-days that recovered larvae experienced in the field and the degree-days for larvae to develop to the same age under lab conditions (King et al. 1975) multiplied by the entire larval developmental duration under lab conditions. The same approach was used to estimate larval developmental variability. Survival of sugarcane borer larvae from hatching to ca. 18 days old was estimated by the ratio of the number of recovered larvae and the egg release rate. Parasitization by *C. flavipes* was similarly estimated as the ratio of the number of parasitized larvae and the number of recovered larvae.

Analyses of variance (ANOVAs) were conducted on larval developmental duration, survival, proportion parasitized, *C. flavipes* progeny produced per parasitized larva, and *C. flavipes* sex ratio, with up to 5 independent variables and their associated interactions for each (Table 3.1). The survival rate and proportion parasitized were log transformed to meet the assumptions of normality. ANOVAs were also conducted on simulated cumulative seasonal damaging larval density, seasonal maximum density of *C. flavipes* adults produced by the released parasitoids, seasonal maximum proportion parasitized, rice yield, and economic value of *C. flavipes* release (see Eq. 3.11), each as affected by year, overwintering larvae density, *C. flavipes* release rate and release timing, and the corresponding interactions.

Table 3.1. Main factors used in the ANOVAs of developmental duration of sugarcane borer larvae, larval survival, proportion parasitized, number of *C. flavipes* progeny per parasitized larvae, and sex ratio of *C. flavipes* progeny

Response Variable	Main Factors			
	Year	Cultivar	Stage	Initial Egg Density
Developmental Duration of Sugarcane Borer Larvae	X	X	X	
Larval Survival	X	X	X	X
Proportion Parasitized	X	X	X	X
Number of *C. flavipes* Progeny per Parasitized Larvae	X	X	X	
Sex Ratio of *C. flavipes* Progeny	X	X	X	

Results for each ANOVA were expressed as $\bar{x} \pm s.d.$ Main factors or interactions with $P < 0.05$ were considered to be statistically significant. For ANOVAs conducted on field data, statistically significant main factors and interactions that explained more than 5% of variability were discussed in detail. For ANOVAs conducted on simulated results and economic value, all main factors and interactions that were statistically significant were discussed in detail.

Results and Discussion

Field and Lab Experiments. A total of 2,710 and 722 sugarcane borer larvae were recovered in 2005 and 2006, respectively. In 2005, 13 larvae were recovered from the zero control treatment, which implied a low level of natural infestation that year.

Sugarcane borer larval developmental duration was significantly affected by year, stage, cultivar, and year × stage interaction (Table 3.2). Developmental duration was greater in 2005 (658.0 ± 51.8 DD) than in 2006 (545.1 ± 86.6 DD), and was greater at 3rd tiller (611.5 ± 51.1 DD) and panicle differentiation (639.9 ± 76.8 DD) than at heading (548.5 ± 94.9 DD). Developmental duration was greater in Francis (631.7 ± 80.0 DD) than in Cocodrie (587.9 ± 78.9 DD) and Jefferson (580.6 ± 94.2 DD). In 2005, developmental duration was greater at panicle differentiation (709.1 ± 28.4 DD) than at 3rd tiller (636.8 ± 82.8 DD) and heading (625.0 ± 56.3 DD). In contrast, in 2006, developmental duration was greater at 3rd tiller (593.7 ± 95.0 DD) and panicle differentiation (566.4 ± 79.3 DD), followed by heading (467.9 ± 79.4 DD). The estimated developmental duration ranged from 40.5% to 85.5% longer than under lab conditions.

Larval survival was affected by year, stage, density, stage × density, and year × cultivar × density interactions. Survival was higher in 2005 (0.144 ± 0.106) than in 2006 (0.034 ± 0.055), and was higher at 3rd tiller (0.160 ± 0.126) than at panicle differentiation

(0.051 ± 0.055) or heading (0.056 ± 0.063). In contrast, in an open-field experiment immediately adjacent to the present experiment, survival 18 days after release at 3rd tiller was much lower (0.024), likely due to rainfall-induced mortality occurring to larvae prior to their entering the stems (Lv et al. 2008), and wind-induced mortality, which is suspected to cause early instars to be blown into the floodwater. Both rainfall and wind were reduced inside the mesh cloth field cages. Wind speed measured in an empty cage using a Mannix DCFM8906 CFM Master Air Flow Meter was reduced by ca. 23.5% (Eq. 3.12). The wind speed would likely have been even further reduced had plants been growing in the cage.

$$W_{in} = Max\left(0, -0.528 + 0.765W_{out}\right) \quad R^2 = 0.974,\ df = 1,\ 8,\ P < 0.001 \qquad (3.12)$$

where:

W_{in} = wind speed within the polyester cage (m s^{-1})

W_{out} = wind speed outside the polyester cage (m s^{-1})

A total of 79 and 98 parasitized larvae were recovered in 2005 and 2006, respectively. None of the larvae from the zero control split-split plots in 2005 were parasitized. Parasitization was significantly affected by year and crop growth stage (Table 3.2). The proportion parasitized was higher in 2006 (0.105 ± 0.214) than in 2005 (0.054 ± 0.151), which was a result of the higher parasitoid release rate in 2006. The highest parasitism was observed at 3rd tiller (0.119 ± 0.201), followed by panicle differentiation (0.073 ± 0.203) and heading (0.025 ± 0.108).

Table 3.2. ANOVAs for developmental duration of sugarcane borer larvae, larval survival, proportion parasitized, number of progeny per parasitized larvae, and sex ratio of *C. flavipes* progeny

Source of Variances	Development Duration of Sugarcane Borer Larvae				Larval Survival				Proportion Parasitized				Number of Progeny per Parasitized Larvae				Sex Ratio of *C. flavipes* Progeny			
	df	F	P > F	% Explained Variability	df	F	P > F	% Explained Variability	df	F	P > F	% Explained Variability	df	F	P > F	% Explained Variability	df	F	P > F	% Explained Variability
Year	1	94.98	~ 0	32.1	1	245.09	~ 0	46.8	1	0.77	0.401	0.5	1	0.08	0.789	~ 0	1	1.72	0.192	1.1
Block	2	0.18	0.841	0.1	2	7.07	0.012	2.7	2	0.50	0.622	0.7	2	2.52	0.130	15.0	2	0.19	0.832	0.2
Cultivar	2	10.53	0.004	7.1	2	2.51	0.131	1.0	2	~ 0	0.999	~ 0	2	1.53	0.263	1.9	2	0.93	0.401	1.1
Year × Cultivar	2	2.12	0.171	1.4	2	1.64	0.242	0.6	2	0.14	0.868	0.2	2	1.19	0.345		2	0.68	0.509	0.8
Error (1)	10				10				10				10				11			
Stage	2	26.39	~ 0	25.6	2	41.44	~ 0	22.8	2	4.76	0.019	5.1	2	0.88	0.416	83.2	2	0.09	0.913	0.1
Year × Stage	2	15.40	~ 0	15.0	2	0.60	0.559	0.3	2	2.02	0.156	2.2	2	0.02	0.981	~ 0	2	0.54	0.586	0.7
Cultivar × Stage	4	1.74	0.175	3.4	4	1.78	0.166	2.0	4	0.55	0.702	1.2	4	0.80	0.530	6.2	4	0.18	0.947	0.4
Year × Cultivar × Stage	4	0.08	0.989	0.2	4	0.93	0.463	1.0	4	0.22	0.926	0.5	3	0.13	0.943	~ 0	2	0.42	0.659	0.5
Error (2)	24				24	5.62			23				140				145			
Density					3	26.76	~ 0	3.9	3	0.94	0.427	1.0								
Year × Density					3	2.56	0.059	0.4	3	0.58	0.632	0.6								
Cultivar × Density					6	1.05	0.399	0.3	6	1.32	0.259	2.8								
Stage × Density					6	2.98	0.010	0.9	6	1.67	0.137	3.6								
Year × Cultivar × Density					6	4.94	~ 0	1.5	6	0.62	0.713	1.3								
Year × Stage × Density					6	1.53	0.175	0.5	6	1.73	0.125	3.7								
Cultivar × Stage × Density					12	1.68	0.082	1.0	12	0.69	0.755	2.9								
Year × Cultivar × Stage × Density					12	1.32	0.218	0.8	12	0.52	0.897	2.2								
Error (3)					108				87											

Alam (1980) reported *C. flavipes* parasitized an average of ca. 5 sugarcane borer larvae per female. Potting et al. (1997) reported *C. flavipes* allocated ca. 80% of its eggs parasitizing 3 larvae and were depleted of eggs after parasitizing 4 or 5 larvae. In contrast, Wiedenmann et al. (1992) reported 28% failed to parasitize any larvae, 69% parasitized 1 larva, and 3% parasitized 2 larvae. In our lab experiment, 35%, 50%, and 15% *C. flavipes* females parasitized 0, 1, and 2 sugarcane borer larvae, respectively, with a maximum average of 0.961 larvae parasitized by each *C. flavipes* observed at 28.0 ºC. In contrast, the average number of larvae parasitized per *C. flavipes* in the field cages was 0.15 in 2005 and 0.04 in 2006.

Potting et al. (1997) reported 30%-40% of *C. flavipes* females were killed by the spitting and biting of stem borer larvae when larvae were confined within artificial tunnels. The majority of *C. flavipes* were killed if they approached the larvae from the head end. Takasu and Overholt (1997) reported parasitoid mortality due to aggressive defensive behavior was significantly higher when older larvae were attacked, with 26.7, 53.3, and 66.7% of *C. flavipes* killed when attacking 3rd, 4th, and 5th instars, respectively. In our study, *C. flavipes* showed greater oviposition preference for large larvae, which should result in a higher risk of being killed.

The lower proportion parasitized in the field experiment was caused by a low effective parasitoid search rate, likely due to the larvae being concealed in tunnels within stems. The effective search rate estimated from the field experiment is 49 cm^2 ground area per day (2.21 tillers d^{-1}) per parasitoid (Fig. 3.2). Rice has smaller stems in comparison to many sugarcane borer host plants, such as sugarcane, corn, and sorghum.

When *C. flavipes* females are exposed to frass under laboratory conditions, they generally spend 5-15 min seeking an opening to the larval tunnel before giving up (Potting et al. 1999). When larvae feed inside rice stems, the tunnels are often blocked by frass, which can prevent *C. flavipes* from reaching them (Lv personal observation).

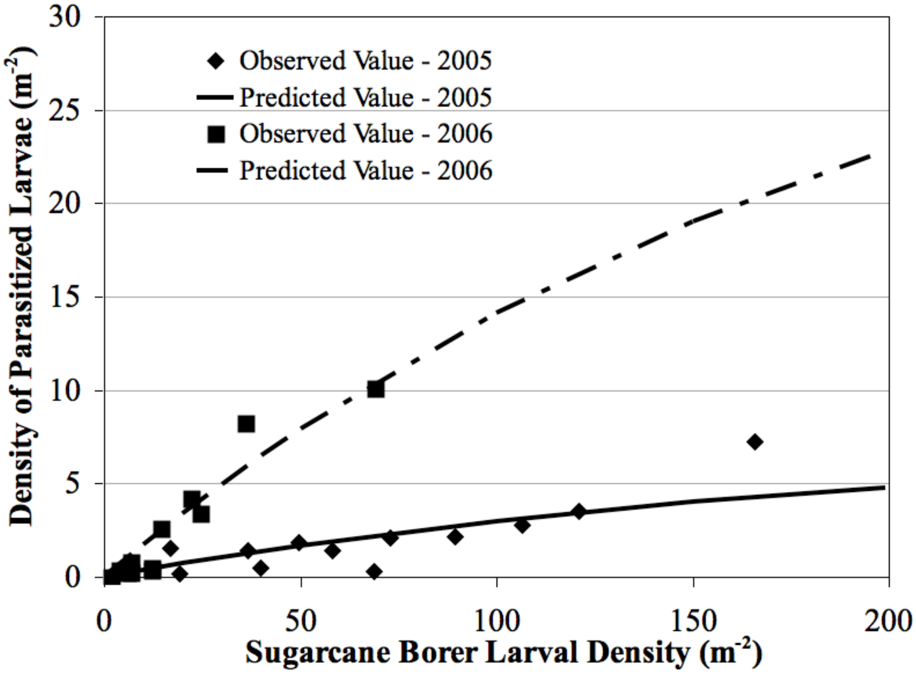


Fig. 3.2. Field estimated functional response of *C. flavipes* on sugarcane borer larvae, as affected by both host and parasitoid densities. The density of *C. flavipes* females was 8 and 40 m^{-2} in 2005 and 2006, respectively.

Plant host-specific kairomones also affect the ability of *C. flavipes* to detect prey. Mohyuddin et al. (1981) indicate *C. flavipes* detects host larvae by the presence of kairomones in the larval frass. Inayatullah (1983) showed frass produced by four stem borer species feeding on sugarcane was less preferred by *C. flavipes* than frass produced by the same species feeding on sorghum (*Sorghum bicolor* Moench), corn (*Zea mays* L.), pearl millet (*Pennisetum typhoides* Stapf and Hubbard), and *Sorghum sudanense* Stapf. Ngi-song et al. (2000) identified 6 components in volatiles that are attractive to *C. flavipes* females: (Z)-3-hexenyl acetate, linalool, (E)-4,8-dimethyl-1,3,7-nonatriene, heptanal, (E)-β-ocimene, and a C-5 aliphatic compound. The relative preference shown by *C. flavipes* for stem borer frass produced on rice is not known.

Significant main effects and interactions were not observed for either *C. flavipes* progeny produced per parasitized larva or *C. flavipes* sex ratio (Table 3.2). Parasitized larvae produced an average of 27.9 ± 19.1 *C. flavipes* adults, with 5.1% of the larvae parasitized by unfertilized females. The mean sex ratio produced by fertilized *C. flavipes* was 2.57:1 (females:males), with a 2.13:1 sex ratio recorded for all females combined. The average number of *C. flavipes* progeny per parasitized larva was lower than reported in previous studies, which ranged from 35 to 53 (Alam 1980, Potting et al. 1997, Wiedenmann et al. 1992). Similarly, the progeny sex ratio was considerably lower than previously reported (Potting et al. 1997, Wiedenmann et al. 1992). Takasu and Overholt (1997) reported the majority of *C. flavipes* adults killed by sugarcane borer larval defensive behavior completed parasitism successfully. However, it is unknown whether the defensive behavior of host larvae reduces the clutch size. The oviposition behavior generally takes several seconds (Potting et al. 1997). In our lab experiment, sugarcane borer larvae were observed interrupting *C. flavipes* ovipositioning ca. 10% of the time.

Simulation Analyses. Parameters used by the simulation model are presented in Tables 3.3 and 3.4. Table 3.3 summarizes statistics for minimum developmental duration, maximum fecundity, and sex ratio for the sugarcane borer and *C. flavipes*, and the oviposition preference for each host instar, effective search rate, and the maximum number of host parasitized per *C. flavipes*. Table 3.4 summarizes parameters used to estimate sugarcane borer developmental duration and fecundity, and maximum number of hosts parasitized per *C. flavipes*, each as a function of temperature, with sugarcane borer survival also a function of host plant age and rainfall.

The simulated seasonal cumulative damaging larval density, seasonal maximum parasitoid adult density, and seasonal maximum proportion host parasitized were each affected by year, overwintering larval density, parasitoid release rate, timing of release, and all two-way interactions (Table 3.5). The highest seasonal cumulative damaging larval density (716.9 ± 401.3 m^{-2}) was simulated in 1978, while the lowest (30.1 ± 16.0 m^{-2}) was in 1998. Year as a variable resulted in a 23.8-fold range in seasonal cumulative damaging larval density, which contributed 56.7% of the total variability for this response variable. When temperatures are low during larval diapause, as evident by lower rates of DD accumulation, larvae terminate diapause later in the year, adults emerge later from overwintering, and eggs are laid on rice plants at later crop growth stages, which afford higher survival of subsequent larvae and higher seasonal cumulative damaging larval densities (Fig. 3.3). Moths are assumed to deposit eggs on rice, even when the plants are small and larval survival is close to zero. This assumes alternative weed hosts for the sugarcane borer are limited early in the spring, which is consistent for most grassy weed hosts for the Upper Gulf Coast region of the U.S.

The highest seasonal maximum parasitoid adult density (458.5 ± 647.9 m^{-2}) and the highest seasonal maximum proportion parasitized (0.403 ± 0.380) were observed in 1978, while the lowest were observed in 1998 (4.62 ± 6.30 m^{-2}, 0.027 ± 0.021). Year

Table 3.3. Summary of statistics for minimum developmental duration, maximum fecundity, and sex ratio for the sugarcane borer and *C. flavipes*, and the oviposition preference for each host instar, effective search rate, and the maximum number of host parasitized per *C. flavipes*

Life Table Parameters	Sugarcane Borer				*C. flavipes*	
	Egg	Larval	Pupal	Adult	Immature	Adult
Minimum Developmental Duration (DD > 10.4°C)	86.2	562.0	123.8	103.3	277.4	69.8
Variance of the Developmental Duration	14.2	8236.3	72.5	279.5	67.2	53.29
Temperature (°C) when the Minimum Developmental Duration was Observed	26.99	27.08	27.03	28.04	-	-
Maximum Fecundity	-	-	-	427.1	-	26.7
Temperature (°C) when the Maximum Fecundity was Observed	-	-	-	24.33	-	-
Proportion of Female Offspring	0.50				0.72	
Oviposition preference 1st Instar	-	-	-	-	-	0
2nd Instar	-	-	-	-	-	0.337
3rd Instar	-	-	-	-	-	0.385
4th Instar	-	-	-	-	-	0.718
5th Instar	-	-	-	-	-	1
Effective Search Rate ($m^2d^{-1}female^{-1}$)	-	-	-	-	-	0.0049
Maximum Daily Parasitization per Female	-	-	-	-	-	0.961
Temperature (°C) when Maximum Daily Parasitization per Female was observed	-	-	-	-	-	28.02

Table 3.4. Parameters used to estimate sugarcane borer developmental duration and fecundity, and maximum number of host parasitized per *C. flavipes*, each as a function of temperature, and sugarcane borer survival as a function of temperature, host plant age, and rainfall

Submodel	Function	Stage	Equation	Parameter	Estimate	r^2	df	P > F
Sugarcane Borer	Developmental Duration	Egg	1	β_1	-0.794	0.837	2,3	0.066
				β_2	1.721			
	Developmental Duration	Larval	1	β_1	-0.015	0.975	2,3	0.004
				β_2	17.754			
	Developmental Duration	Pupal	1	β_1	-0.536	0.909	2,3	0.027
				β_2	2.297			
	Developmental Duration	Adult	1	β_1	0.159	0.266	2,3	0.628
				β_2	2.467			
	Diapause Induction	Larval	4a	β_5	21.07	0.921	2,3	0.022
				β_6	-0.78			
				β_7	-1.64	0.861	2,3	0.052
				β_8	0.06			
	Intrinsic Survival	Egg - Adult	5a	β_9	0.964	0.954	4,10	~ 0
				β_{10}	-0.323			
				β_{11}	10.142			
				β_{12}	0.344			
	Host Plant Induced Survival	Larval	5b	β_{13}	0.024	0.986	4,2	0.028
				β_{14}	112.663			
				β_{15}	25.793			
				β_{16}	0.287			
	Rainfall Induced Survival	Egg, Larval	5c	β_{17}	-0.359	0.953	1,4	0.001
	Age Cumulative Fecundity	Adult	6a	β_{18}	0.228	~ 1	2,6	~ 0
				β_{19}	-0.512			
	Fecundity as Affected by Temperature	Adult	6b	β_{20}	-1.966	0.985	2,4	~ 0
				β_{21}	-1.476			
C. flavipes	Maximum Number of Hosts Parasitized per Female as Affected by Temperature	Adult	8c	β_{22}	0.028	0.736	2,2	0.264
				β_{23}	1.920			

Table 3.5. ANOVAs for simulated seasonal cumulative damaging larval density, seasonal maximum number of *C. flavipes* adults, seasonal maximum proportion host parasitized, yield, and economic value

Source of Variances	df	Seasonal Cumulative Damaging Larval Density			Seasonal Maximum Number of *C. flavipes* Adults			Seasonal Maximum Proportion Host Parasitized			Yield			Economic Value		
		F	P > F	% Explained Variability	F	P > F	% Explained Variability	F	P > F	% Explained Variability	F	P > F	% Explained Variability	F	P > F	% Explained Variability
Year	29	2782.31	~ 0	56.33	304.04	~ 0	20.04	507.13	~ 0	22.44	2942.20	~ 0	57.54	149.46	~ 0	6.23
Overwintering Larval Density	9	3715.72	~ 0	23.35	456.22	~ 0	9.33	1019.53	~ 0	14.00	3726.61	~ 0	22.62	283.10	~ 0	3.66
C. flavipes Release Rate	10	44.38	~ 0	0.31	83.37	~ 0	1.71	337.30	~ 0	4.63	56.78	~ 0	0.38	3515.82	~ 0	45.47
Overwintering Larval Density × *C. flavipes* Release Rate	90	2.40	~ 0	0.15	4.60	~ 0	0.85	6.48	~ 0	0.80	2.61	~ 0	0.16	4.16	~ 0	0.48
Timing of *C. flavipes* Release	7	217.27	~ 0	1.06	482.90	~ 0	7.68	1300.02	~ 0	13.89	233.28	~ 0	1.10	620.36	~ 0	6.24
Overwintering Larval Density × Timing of *C. flavipes* Release	63	15.13	~ 0	0.67	44.00	~ 0	6.30	76.91	~ 0	7.39	13.47	~ 0	0.57	35.81	~ 0	3.24
C. flavipes release rate × Timing of *C. flavipes* Release	70	4.48	~ 0	0.22	6.11	~ 0	0.87	11.63	~ 0	1.12	6.34	~ 0	0.30	10.77	~ 0	0.98
Overwintering Larval Density × *C. flavipes* Release Rate × Timing of *C. flavipes* Release	630	0.27	~1	0.12	0.43	~1	0.56	0.41	~1	0.36	0.32	~1	0.13	0.48	~1	0.39
Error	25491															

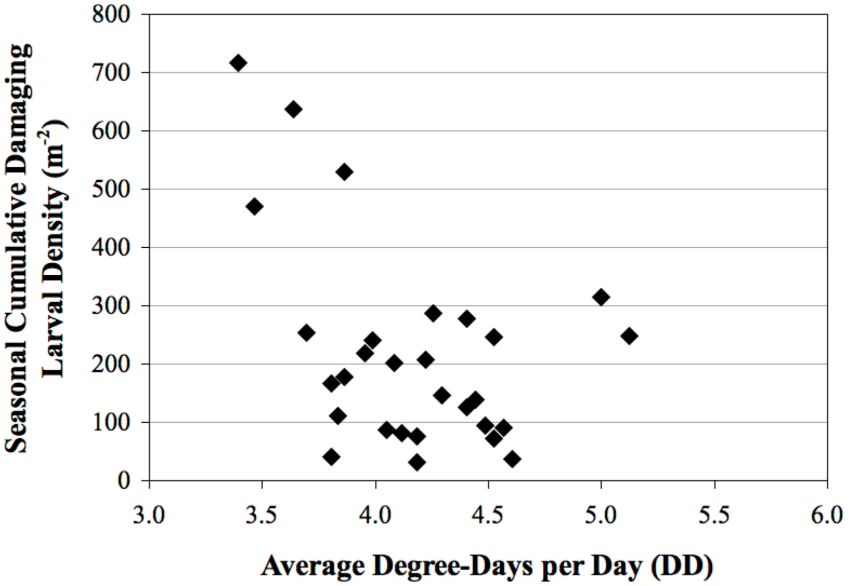


Fig. 3.3. Simulated seasonal cumulative damaging larval density (m^{-2}) as affected by the average degree-days (DD > 10.4 ºC) per day during larval diapause for 1978 to 2007.

resulted in a 99.1-fold range in seasonal maximum parasitoid adult density (20.0% explained variability) and a 14.9-fold range in seasonal maximum proportion parasitized (22.4% explained variability. When simulated early season larval densities were higher, *C. flavipes* densities increased more rapidly, and higher seasonal maximum proportions parasitized were observed in later generations.

Seasonal cumulative damaging larval density increased from 42.8 ± 35.2 m^{-2} to 383.2 ± 311.5 m^{-2} when overwintering larval density increased from 1 to 10 m^{-2} (Fig. 3.4a), and decreased from 243.6 ± 260.8 m^{-2} to 202.2 ± 206.6 m^{-2} when parasitoid

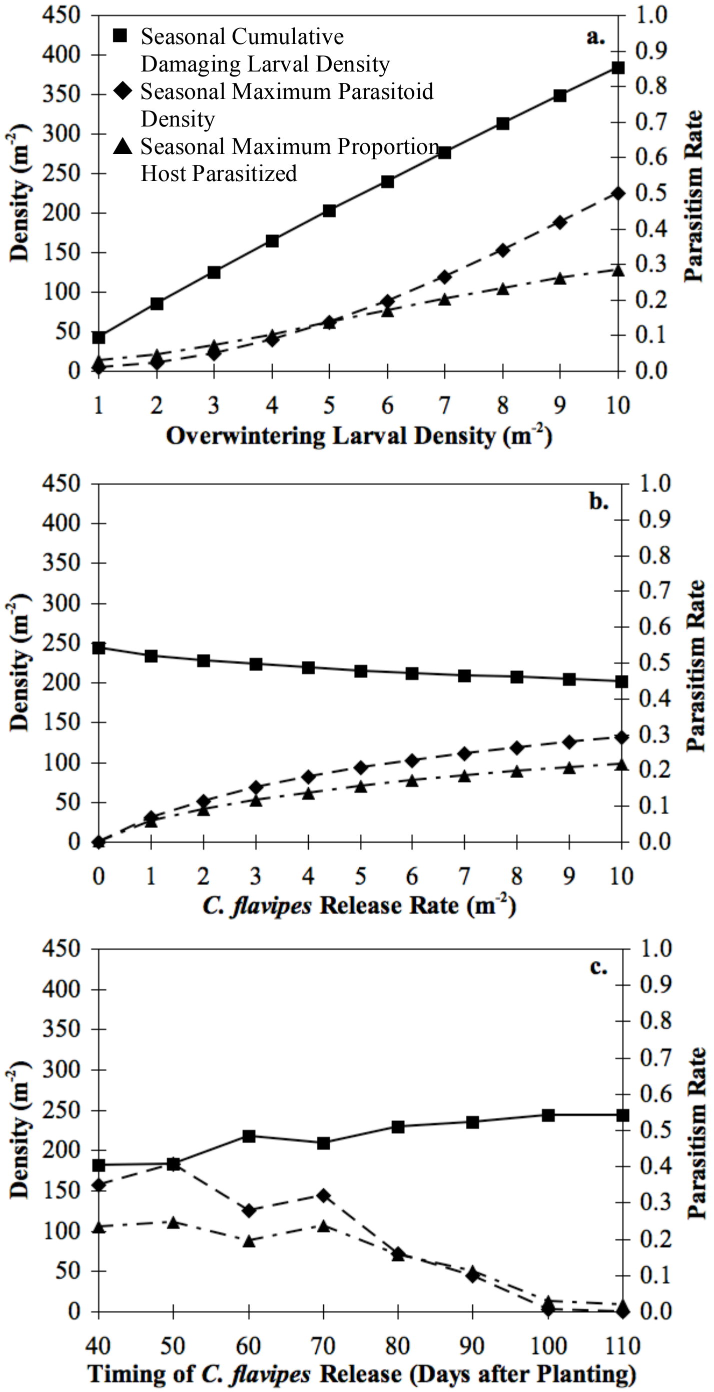


Fig. 3.4. Simulated seasonal cumulative damaging larval density, seasonal maximum number of *C. flavipes* adults, and seasonal maximum proportion host parasitized, each as affected by a) overwintering larval density, b) *C. flavipes* release rate, and c) timing of *C. flavipes* release.

release rate increased from 0 to 10 m^{-2} (Fig. 3.4b). The seasonal maximum *C. flavipes* female density and the seasonal maximum proportion host parasitized increased from 3.7 ± 6.6 to 225.1 ± 415.9 m^{-2} and 0.029 ± 0.021 to 0.285 ± 0.313, respectively, when overwintering larval density increased from 1 to 10 m^{-2} (Fig. 3.4a), and increased from 0 to 130.9 ± 293.0 m^{-2} and 0 to 0.218 ± 0.262, respectively, when release rate increased from 0 to 10 m^{-2} (Fig. 3.4b).

The seasonal cumulative damaging larval density was lowest (181.9 ± 162.4 m^{-2}) when parasitoids were released 40 days after planting and highest (243.3 ± 260.4 m^{-2}) when released 110 days after planting (Fig. 3.4c). *Cotesia flavipes* was most effective when released during the 1st sugarcane borer larval generation, providing 25.3% average reduction in the seasonal cumulative damaging larva density. The highest seasonal maximum *C. flavipes* adult density (183.7 ± 377.4 m^{-2}) and the highest seasonal maximum proportion host parasitized (0.247 ± 0.303) were observed when parasitoids were released 50 days after planting, while the lowest seasonal maximum parasitoid adult density (ca. 0 m^{-2}) and the lowest seasonal maximum proportion host parasitized (0.018 ± 0.015) were observed when parasitoids were released 110 days after planting (Fig. 3.4c). The difference in developmental duration resulted in a minor but varying degree of asynchrony between parasitoid adult emergence and host larval availability.

Simulated yield was affected by year, overwintering larval density, *C. flavipes* release rate, timing of release, and all 2-way interactions (Table 3.4). The lowest yield (1,481.2 ± 2,130.0 kg ha^{-1}) was in 1978, representing a 78.1% yield loss. The highest yield (7,153.0 ± 183.1 kg ha^{-1}) was in 1998, which was ca. 5.5% higher than the yield of uninjured rice fields (6776.4 kg ha^{-1}). Yield decreased from 6,781.2 ± 461.1 kg ha^{-1} to 3,732.8 ± 2,313.6 kg ha^{-1} when overwintering larval density increased from 1 to 10 m^{-2}. Yield compensation was detected at the lowest overwintering larval density (1 m^{-2}), while yield was reduced by an average of ca. 44.9% at the highest overwintering larval density (10 m^{-2}).

Simulated yield increased from 4,906.3 ± 2,179.6 kg ha^{-1} to 5,296.9 ± 1,827.2 kg ha^{-1} when parasitoid release rate increased from 0 to 10 m^{-2}. Yield was highest when parasitoids were released 40 days after planting (5,463.9 ± 1,583.9 kg ha^{-1}), and lowest when parasitoids were released 110 days after planting (4,910.5 ± 2176.2 kg ha^{-1}). When averaged across years, the maximum *C. flavipes* release rate and earliest timing of release reduced yield loss by 20.9% and 29.8%, respectively. When *C. flavipes* were released at the earliest simulated time (40 days after planting) and maximum rate, yield increased to an average of 5,857.6 ± 984.6 kg ha^{-1}, representing a 50.9% reduction of yield loss (Fig. 3.5a).

Economic Value of Larval Injury. The economic value of *C. flavipes* release was affected by year, overwintering larval density, *C. flavipes* release rate, timing of release, and all 2-way interactions (Table 3.4). However, positive economic value was only observed at the 3 highest overwintering larval densities (8, 9, and 10 m^{-2}) at the two earliest releases (Fig. 3.5b). When averaged across years, the greatest positive economic value was \$118.03 ± 202.28 ha^{-1}, when the overwintering larval density was 10 m^{-2}, and *C. flavipes* was released 50 days after planting at a rate of 2 females m^{-2}.

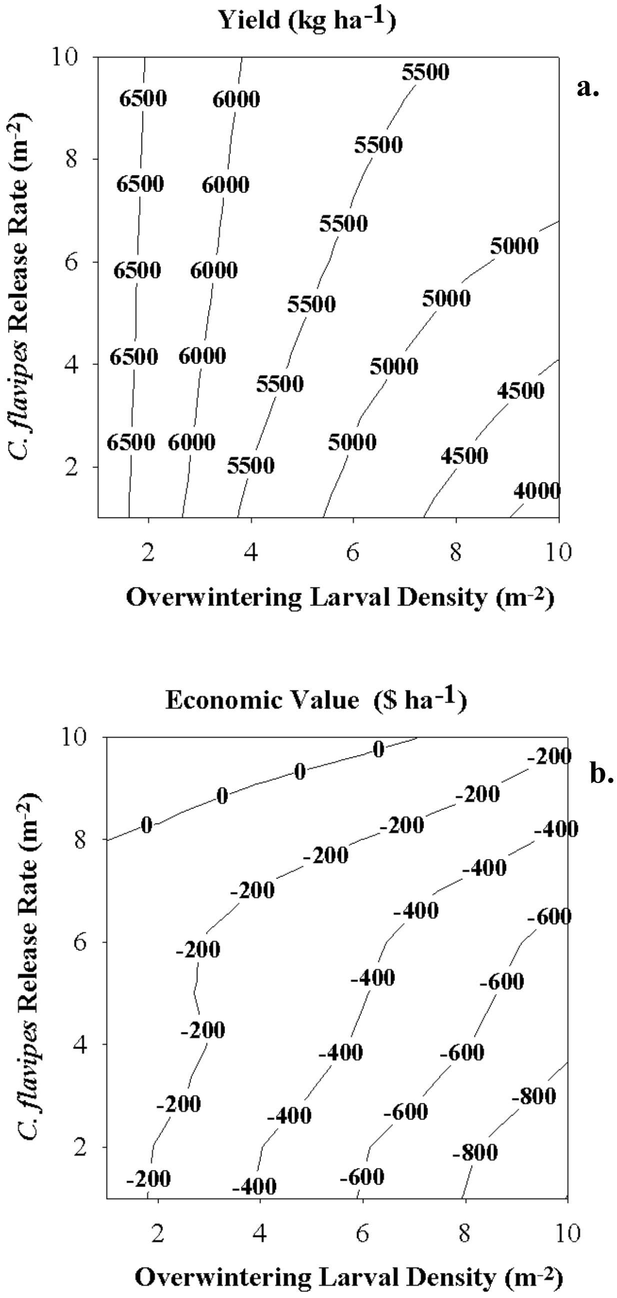


Fig. 3.5. Simulated a) rice yield and b) economic value from *C. flavipes* release, each as affected by overwintering larval density and release rate, with parasitoids released at the optimal timing.

For an augmentative release to be economical, the savings must be comparable to that achieved using currently available control methods. Sugarcane borer management in rice in subtropical-temperate regions is entirely achieved through the use of insecticides. Two applications of one of the pyrethroids: gamma-cyhalothrin (Prolex™), lambda-cyhalothrin (Karate Z®), or zeta-cypermethrin (Mustang MAX™) are commonly used in Texas, one each at 1” to 2” panicle and early heading, and are estimated to reduce whiteheads by 87.6% (Way et al. 2006) at a cost of \$67 ha^{-1}. Reay-Jones et al. (2007) assumed the reduction in *D. saccharalis* injury due to insecticide-based control was proportional to the reduction in whitehead injury. If this assumption is correct, incorporating insecticide mortality into the sugarcane borer model resulted in an economic benefit ranging from \$184.80 ± 161.19 ha^{-1} to \$1319.30 ± 807.22 ha^{-1}, when overwintering larval density range from 1 to 10 m^{-2}, respectively.

The economic analysis suggests *C. flavipes* is an inefficient biocontrol agent for the sugarcane borer in rice and does not provide economic control in subtropical-temperate climatic regions such as those found in Beaumont, Texas. Its inefficiency in this area is due to a low effective search rate, a low maximum daily parasitism per female, and, most importantly, an asynchrony with its hosts due to early emergence of first generation females that prevents them from finding and parasitizing first generation hosts in significant numbers (White et al. 2004). Its inability to provide economic control is due to these factors in addition to its high rearing cost.

In contrast, *C. flavipes* has been reported to provide successful biocontrol of the sugarcane borer in subtropical (Alam et al. 1971, Meagher et al. 1998) and tropical

(Macedo et al. 1993) climatic regions. *Cotesia flavipes* has also been successfully introduced to Africa, with parasitism of stem borers by *C. flavipes* reported in Ethiopia, Kenya, Mozambique, South Africa, Tanzania, Uganda, and Zimbabwe (Omwega et al. 1997, Cugala et al. 1999, Zhou and Overholt 2001, Chinwada et al. 2002, Cugala and Omwega 2002, Matama-Kauma et al. 2002, Getu et al. 2003). The three most important stem borer species in Africa are *Chilo partellus* (Swinhoe), *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae), and *Busseola fusca* Fuller (Lepidoptera: Noctuidae). *Cotesia flavipes* has the greatest preference for *C. partellus*, followed by *S. calamistis* and *B. fusca* (Cugala et al. 1999, Matama-Kauma et al. 2002, Getu et al. 2003). The availability of multiple host species combined with a climate that allows year-around population activity undoubtedly increases the chance for *C. flavipes* population establishment in East Africa.

The density of *C. flavipes* is generally sufficient within 3 to 4 years of release to maintain sugarcane borer densities below economic injury levels in subtropical regions (White and Reagan 1999). Zhou and Overholt (2001) showed stem borer parasitism by *C. flavipes* remained at a low level in Kenya until four years after release, at which time it increased rapidly to ca. 50%. Matama-Kauma et al. (2001) reported stem borer parasitism by *C. flavipes* increased to 20% 2 years after release in Uganda, but less quickly in other countries in East Africa. The reason for variation in the parasitism rates was not identified. In subtropical-temperate regions, opportunity may exist for the selection of *C. flavipes* biotypes that emerge later in the spring in areas having colder climates; however, such biotypes have not been identified to date.

In the absence of a *C. flavipes* population that is climatically adapted, are other parasitoids available for augmentative release to control the sugarcane borer in a temperate-subtropical environment? Three additional parasitoid species, *L. diatraeae*, *T. fuentesi*, and *T. galloi*, have been tested and found to show promise (Alam 1980, Browning and Melton 1987, Parra and Zucchi 2004). Between the three, *T. galloi* has been studied the most extensively. *Trichogramma galloi* offers at least three advantages as a possible biocontrol agent contrasted to *C. flavipes*. Firstly, commercial rearing of *Trichogramma* has been well developed and is relatively inexpensive ($5.00 per 10,000 parasitoids, M. P. Hoffmann, personal communication) compared to *C. flavipes* ($100.00 per 10,000 parasitoids). Secondly, *Trichogramma* spp. have relatively high host search rates, and as a result are able to find prey at relatively low densities. Thirdly, *Trichogramma* are egg parasitoids, and parasitized eggs fail to produce damaging larvae.

To evaluate the economic value of using *T. galloi* to control the sugarcane borer, estimates of developmental duration, parasitoid searching rate, and maximal proportion parasitized were obtained from the literature, and incorporated into the parasitoid model. The developmental threshold for *T. galloi* is 13.6 ˚C (Cônsoli and Parra 1996). The developmental duration for immatures (128.6 ± 9.1 DD) and adults (81.1 ± 15.2 DD) were estimated using data from Cônsoli and Parra (1996), as were the cumulative maximum number of hosts parasitized per female ($b_{c,i,}$) and age class specific maximum number of hosts parasitized per a female (Eqs. 13a-b, which equals b in Eq. 3.8).

$$b_{c,i} = 49.10\left(\frac{i}{n_a}\right)^{0.87\left(\frac{i}{n_a}\right)^{-0.71}} \qquad R^2 = 0.971, \quad df = 2{,}11, \quad P < 0.001 \qquad (3.13a)$$

$$b = b_{c,i} - b_{c,i-1} \tag{3.13b}$$

where:

n_a = number of age classes in adult stage

Pereira-Barros et al. (2005) show each parasitized sugarcane borer egg produced an average of 2.29 *T. galloi* progeny, with a 1.55:1 sex ratio. Field estimates of the effective search rate for *T. galloi* are not available from the literature, but was estimated as 0.0201 m^2 day^{-1} $female^{-1}$, using average field cage estimates for 3 *Trichogramma spp.* parasitizing Asian corn borer, *Ostrinia furnacalis* (Guenée) (Lepidoptera: Pyralidae) (Zhang et al. 2004).

Ten overwintering larval densities and 8 timings of release were simulated for 30 years (1976-2006). The simulated release rate of *T. galloi* was 4.1 females m^{-2} (6.7 males + females m^{-2}). With this release rate, the cost of using *T. galloi* equals the cost of insecticide-based control. Analysis of variance was conducted on the economic value as affected by year, overwintering larval density, and timing of release.

Economic value was significantly affected by overwintering larval density ($df_1 = 9$, $df_2 = 2{,}399$, $F = 80.37$, $p < 0.001$), timing of release ($df_1 = 9$, $df_2 = 2{,}399$, $F = 150.69$, $p < 0.001$), and the 2-way interaction ($df_1 = 63$, $df_2 = 2{,}292$, $F = 5.37$, $p < 0.001$). The greatest economic value was observed when *T. galloi* were released 50 or 60 days after planting, with 94.6% of eggs parasitized before main crop harvest at high overwintering larval densities (> 5 m^{-2}). The economic value increased from \$30.64 ± 107.46 ha^{-1} to \$1128.75 ± 805.50 ha^{-1} when overwintering larval density increased from 1 to 10 m^{-2}

(Fig. 3.6). The difference between the economic benefit provided by insecticide-based control and the simulated release of *T. galloi* ranged between \$159.90 and \$331.11. Although the economic benefit provided by using *T. galloi* is lower than that provided by using two insecticide applications, the release of *T. galloi* can avoid potential problems with pest resistance, resurgence, and secondary pest outbreaks, as induced by insecticide-based control (Luck et al. 1977). The simulation results suggest *T. galloi* has considerable potential as an augmentative biocontrol agent for the

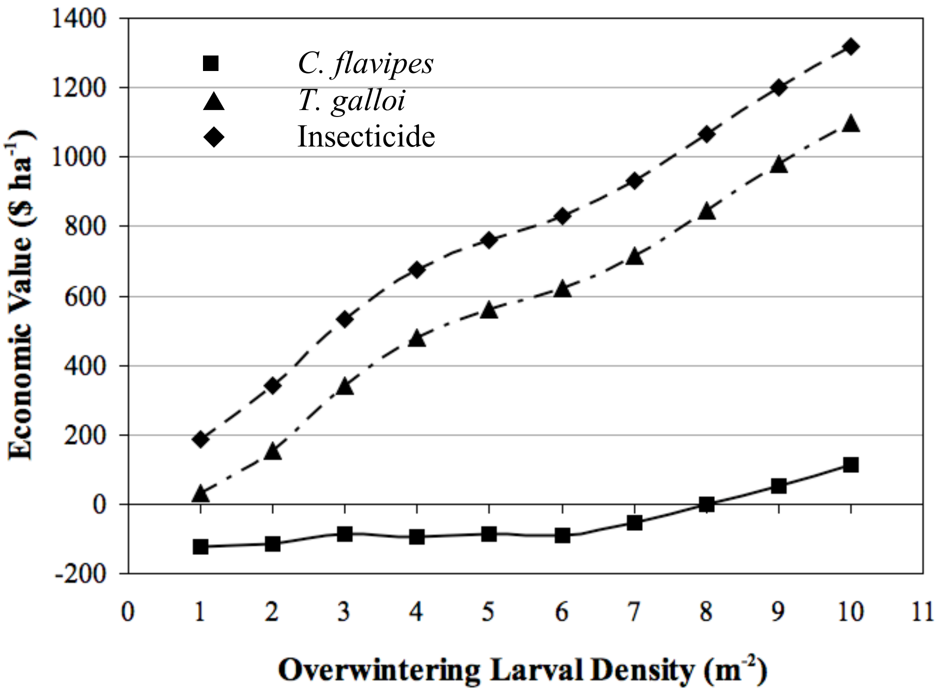


Fig. 3.6. Simulated economic value achieved through insecticide-based sugarcane borer control, augmentative biological control using *C. flavipes* (1 female m^{-2}), or *T. galloi* (4.1 females m^{-2}), each released at the most optimal timing.

sugarcane borer in rice for subtropical-temperate climate regions, especially when the yield loss due to resistance, resurgence, or secondary outbreaks reduces the economic benefit provided by insecticide control to a level lower than that provided by *T. galloi.*

Conclusions

Herein, I investigated the economic benefit of augmentatively releasing *C. flavipes* to control the sugarcane borer. Simulated results suggest seasonal cumulative damaging larval density was negatively correlated with winter temperature, while the seasonal maximum parasitoid density and seasonal maximum proportion parasitized were positively correlated with the seasonal cumulative damaging larval density. The greatest density resulted in ca. 78.1% yield loss. Although *C. flavipes* release reduced sugarcane borer induced yield loss by up to 50.9%, the maximum economic value provided by *C. flavipes* was only $118.03, ca. 7.8% of the maximum economic value provided by insecticides. The inability of augmentatively released *C. flavipes* to provide economic control of the sugarcane borer in temperate-subtropical areas is due to its high rearing cost, a low effective search rate, a low maximum number of hosts parasitized per female, and failure of parasitoids that emerge in the spring to find hosts. These results are in marked contrast to what has been reported for south Texas, Central America, and parts of Africa.

A simulation analysis of augmentatively releasing *T. galloi* suggests this species has the potential to provide up to 94.6% egg parasitization before main crop harvest when released during early crop growth stages. Although *T. galloi* provided lower economic benefit than insecticide-based control, *T. galloi* can avoid potential problems of insecticide-based control. This analysis suggests *T. galloi* may be effective in providing economical control of the sugarcane borer in rice in areas having subtropical-temperate climates. Additional field experiments are required to support these conclusions.

CHAPTER IV

THEORETICAL ANALYSIS OF THE IMPACT OF PARASITOID SEARCH RATE AND HOST-DISCOVERY ON THE EFFECTIVENESS OF AUGMENTATIVE RELEASES USED TO CONTROL LEPIDOPTARAN PESTS

Introduction

Augmentative biocontrol is defined as the periodical release of antagonistic organisms, traditionally predators and parasitoids, to reduce pest population densities below economically injurious levels (van Driesche and Bellows 1996). Hunter (1997) listed more than 130 commercially available natural enemy species in North America. van Lenteren (2003) reported 125 commercially available biocontrol agent species worldwide, among which ca. 30 contribute ca. 90% of the total sales. In contrast, Warner and Getz (2008) listed 38 invertebrate predator and parasitoid species produced by 22 commercial insectaries in North America.

Augmentative biocontrol by most measures is a modestly successful business, having been applied to ca. 15.5 million hectares of agricultural land and forests worldwide (van Lenteren 2000). While van Lenteren (2005) suggests the use of augmentative biocontrol is expected to continue to increase, economic control is far from guaranteed. Batra (1982) indicates more than 90% of augmentatively released biocontrol agents either fail to establish or fail to provide economic control, often due to poor parasitoid or predator performance, unfavorable weather occurring at the time of release, poor timing of introductions relative to the stage of pest population development, or inadequate release rates.

The biocontrol capability of a parasitoid/predator is often estimated using functional response equations, which express parasitism/predation as a function of pest and biocontrol agent density, effective search rate, and maximum daily parasitism/consumption per biocontrol agent (Holling 1959). Numerous functional response analyses have been conducted, with many using data from simple Petri dish arenas, with filter paper serving as the substrate. Results from such experiments have been questioned in terms of whether the estimated search rates mimic what would occur were the prey located on a host plant. Results from Petri dish experiments can greatly overestimate consumption/parasitism rates observed in natural environments. This bias is in part due to the unrealistically high host densities frequently used in Petri dish experiments. When this occurs, the relative amount of time a parasitoid allocates to searching for prey is very low, and parasitism is limited by the female parasitoid's egg load or by handling time. Kaiser (1979, 1983) estimated the predation rate of *Tetranychus urticae* Koch (Acari: Tetranychidae) by *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae), and demonstrated that bias was also due to the unrealistic shape and texture of the experiment arena. Andow and Prokrym (1990) concluded plant size or surface area, structural variation among plant parts, and the complexity of the host plant branching pattern affect the searching efficiency of *Trichogramma nubilale* Ertle and Davis for *Ostrinia nubilalis* (Hübner) (Lepidoptera: Crambidae). Lukianchuk and Smith (1997) reported *Trichogramma minutum* Riley parasitize an equal number of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs on both artificial and natural leaves having a simple leaf structure, but far fewer on both artificial and natural leaves having a compound structure. Gingras et al. (2002) simulated the impact of the factors identified by Andow and Prokrym (1990) on the searching behavior of *Trichogramma* spp., and reported increasing branching complexity had the greatest impact on reducing host parasitism. Gingras and Boivin (2002) indicated branching complexity had a significant impact on parasitism of *E. kuehniella* eggs by *Trichogramma evanescens* Westwood during 4-hour parasitism bouts, but not during 24-hour parasitism bouts, and concluded the parasitoids reach their daily capacity, in terms of egg load, regardless of the plant structure.

The timing of biocontrol agent population increase, either naturally or due to an augmentative release, can have a major impact on the suppression of a host population. Wilson et al. (1991) concluded delayed establishment of generalist predators in cotton was often sufficient to allow spider mite prey to increase to damaging levels prior to their suppression by predators. White et al. (2004) stated *Cotesia flavipes* (Cameron) (Hymenoptera: Braconidae) failed to provide biocontrol in southern Louisiana during years following release because the early emergence of 1st generation parasitoids prevented them from finding and parasitizing overwintered diapausing larvae of *D. saccharalis*. Lysyk (2004) investigated the augmentative biocontrol of *Musca domestica* L. and *Stomoxys calcitrans* (L.) (Diptera: Muscidae) using 2 gregarious parasitoids and 2 solitary parasitoids, and indicated temporal synchrony is more important for solitary parasitoids.

Elzen et al. (2003) indicated the majority of successful field augmentative releases have been achieved by using parasitoids. The most well studied and widely used parasitoids are *Trichogramma* spp., egg parasitoids of multiple lepidopteran pests (van Lenteren 2000, Vail et al. 2001, Elzen et al. 2003). Commercial augmentative releases using *Trichogramma* spp. have been conducted in more than 50 countries, on ca. 15.1 million ha (van Lenteren 2000), representing 97.4% of the area receiving augmentative releases. In contrast, larval and pupal parasitoids, and predators have been released on 0.3 million ha and 0.1 million ha, respectively. While augmentative biocontrol has been biased heavily towards the use of egg parasitoids, studies that compare the potential of parasitoids that prey on different host stages are not available. In addition, based on my review of the parasitoid literature, I am not aware of previous studies that systematically explored the impact of parasitoid oviposition strategy and host concealment on parasitoid functional response parameters.

The present study has two components. The first determines the effect of parasitoid oviposition strategy, host stage and exposure (herein referred to as host stage/exposure), and experimental arena complexity (without and with host plants), on effective search rate and maximum daily parasitism per female, and the impact of parasitoid oviposition strategy and host stage/exposure on parasitoid key life table parameters. The second component integrates the functional response and life table parameters into a tritrophic plant/host/parasitoid simulation model to estimate the economic benefit obtained from augmentative release of hymenopteran parasitoids having solitary or gregarious oviposition strategies, and that attack host stages with different levels of exposure.

Methods and Materials

Functional Response and Life Table Parameter Analyses. Literature reviews were conducted using Google Scholar and the “Agricultural” topic selection of the “LibCat” search engine provided by Texas A&M University Libraries. The key words were “functional response”, “parasitoid”, and “Lepidoptera”. Studies that analyzed parasitism of lepidopteran pests by hymenopteran parasitoids with host and parasitoid density as factors were categorized by parasitoid oviposition strategy (solitary and gregarious parasitoids), host stage/exposure (exposed eggs, exposed larvae, semi-exposed larvae, concealed larvae, and pupae), and experimental arena complexity (without and with host plants). Exposed larvae refers to exophytic pests that feed fully exposed; semi-exposed larvae refers to either exophytic pests that construct a simple shelter (e.g. leaf rollers) or endophytic pests that burrow into host plant leaf and feed on leaf tissues (e.g. leaf miners); and concealed larvae refers to endophytic stem borers.

For experiments without host plants, parasitoids were assumed to search the inner surface area of the arena (bottom, top, and sides of the Petri dish). For experiments with host plants, parasitoids were assumed to search the respective leaves, stems, or leaves and fruiting structure surface areas, depending on the herbivore’s location upon the host plant. The surface area of each plant species at the crop stage used in each experiment was estimated from published plant growth studies conducted at similar latitudes. The leaf surface area contained within a m^2 area was estimated as twice the leaf area index, assuming parasitoids search both the upper and bottom side of leaves, while the stem surface area (A_{stem}) was estimated using Eq. (4.1a), which is based on estimates of stem diameter (d_{stem}), stem length (l_s), and stem density (ρ_{stem}) for each plant species. The surface area of fruiting structures in the i^{th} size category ($A_{fruit,i}$), and when present the surface area of subtending bracts ($A_{sub,i}$), were estimated using Eqs. (4.1b-c), respectively.

$$A_{stem} = \rho_{stem} \pi d_{stem} l_s \tag{4.1a}$$

$$A_{fruit,i} = \rho_{fruit,i} \frac{\pi}{2} \left(w_i^2 + l_i^2 \frac{\cos^{-1}(w_i/l_i)}{\tan\left(\cos^{-1}(w_i/l_i)\right)} \right) \tag{4.1b}$$

$$A_{sub,i} = A_{fruit,i} r_i \tag{4.1c}$$

where:

$\rho_{fruit,\, i}$ = Density of fruit structures in the i^{th} size category (m^{-2})

w_i = Mean width of fruiting structures in the i^{th} size category (m)

l_i = Mean length of fruiting structures in the i^{th} size category (m)

r_i = Ratio of the surface area of fruiting structures and the surface area of subtending leaf-like structures in the i^{th} size category

For each citation, the maximum daily parasitism per female (b) and the effective search rate (s), defined as the maximum plant or arena surface area (m^2) that can be searched by a parasitoid per day, were estimated by iteratively solving the Frazer-Gilbert equation (Frazer and Gilbert 1976) (Eq. 4.2).

$$N_{h,a} = N_h \left(1 - e^{\left(-bN_p/N_h\right)\left(1-e^{-sN_h/b}\right)} \right) \tag{4.2}$$

where:

$N_{h,a}$ = Density of parasitized host (m^{-2} surface area)

N_h = Host density (m^{-2} surface area)

N_p = Parasitoid density (m^{-2} surface area)

The maximum daily parasitism per female and effective search rate were also estimated for each combination of parasitoid oviposition strategy and host stage/exposure. The regressions were weighted by the surface area available for the parasitoids to search in each study to minimize heterogeneity of variance across host density. The greater range in host density that resulted from combining data from the different experiments allowed the use of an incremental F-test to determine whether host density affects the effective search rate (Eq. 4.3).

$$s = \beta_1 + \beta_2 N_h \tag{4.3}$$

where:

β_i = Empirical constants

For each parasitoid species for which functional response parameters were estimated herein, estimates of lower temperature development threshold, immature developmental duration, adult longevity, number of progeny produced per parasitized host, and proportion of female offspring were obtained using Google Scholar and the “Agricultural” topic selection of the “LibCat” search engine provided by Texas A&M University Libraries. When possible, data were obtained from the same lepidopteran host as used for the functional response parameter estimation. In some cases, a complete set of life table parameters were obtained by combining data from several studies. For the parasitoids whose life table parameters are not available from the literature, estimates from taxonomic similar species within the same genus were used.

Incomplete factorial analyses of variances (ANOVAs) were used to estimate the impact of parasitoid oviposition strategy, host stage/exposure, and experimental arena complexity, on the effective search rate and the maximum daily parasitism per female, and the impact of parasitoid oviposition strategy and host stage on each of the key life table parameters. The effective search rates were log transformed to normalize the data. The incomplete aspect of these analyses was due to our not finding examples representing all of the combinations of the main effects. Main factors and interactions were tested using multiple contrasts using the method of Milliken and Johnson (1993). Factors or interactions with $P < 0.05$ were considered to be statistically significant.

Results and Discussion

Functional Response and Life Table Parameter Analyses. A total of 782 papers were identified from the Google Scholar and the LibCat literature searches using the key words “functional response”, “parasitoid”, and “Lepidoptera”. Only 29 papers contained analyses of parasitism of lepidopteran pests by hymenopteran parasitoids with host and parasitoid density as factors. These papers provided 43 datasets, each for an individual parasitoid species, representing 26 hymenopteran species in 4 families, and 18 lepidopteran species in 9 families, with the studies conducted using 7 plant species (Table 4.1). Twenty-two datasets were for solitary parasitoids and 17 for gregarious parasitoids. Nine, 14, 5, 14, and 1 focused on the parasitism of exposed eggs, exposed larvae, semi-exposed larvae, concealed larvae, and pupae, respectively. The pupal

Table 4.1. Summary of the 42 datasets obtained from the literature and used to estimate maximum daily parasitism per female and effective search rate for hymenopteran parasitoids that attack lepidopteran hosts

Lepidopteran Host Species	Host Family	Hymenopteran Parasitoid Species	Parasitoid Family	Host Stage and Exposure	Parasitoid Oviposition Pattern	Experimental Arena Complexity (with /without host plants)	Host Plant	Maximum Daily Parasitism per Female	Effective Search Rate (m^2 surface area day^{-1} parasitoid^{-1})	Data Source
Plutella xylostella L.	Plutellidae	*Trichogramma pretiosum* Riley	Trichogrammatidae	Egg	Solitary	With	Cabbage	19.00	1.056	He et al. 2001
Diatraea saccharalis F.	Crambidae	*Trichogramma* spp.	Trichogrammatidae	Egg	Solitary	With	Corn	5.20	0.144	Zhang et al. 2004
Chilo sacchariphagus Bojer	Crambidae	*Trichogramma chilonis* (Ishii)	Trichogrammatidae	Egg	Solitary	Without	-	17.75	0.007	Reay-Jones et al. 2006
Plutella xylostella L.	Plutellidae	*Trichogramma chilonis* (Ishii)	Trichogrammatidae	Egg	Solitary	Without	-	53.38	0.014	Hirashima et al. 1990b
Ephestia kuehniella Zeller	Pyralidae	*Trichogramma chilonis* (Ishii)	Trichogrammatidae	Egg	Solitary	Without	-	33.01	0.021	Hirashima et al. 1990b
Galleria mellonella L.	Pyralidae	*Trichogramma chilonis* (Ishii)	Trichogrammatidae	Egg	Solitary	Without	-	28.73	0.005	Reay-Jones et al. 2006
Ephestia kuehniella Zeller	Pyralidae	*Trichogramma minutum* Riley	Trichogrammatidae	Egg	Solitary	Without	-	10.20	0.014	Mills and Lacan 2004
Plutella xylostella L.	Plutellidae	*Trichogramma ostriniae* Pang and Chen	Trichogrammatidae	Egg	Gregarious	Without	-	35.59	0.006	Hirashima et al. 1990b
Ephestia kuehniella Zeller	Pyralidae	*Trichogramma ostriniae* Pang and Chen	Trichogrammatidae	Egg	Gregarious	Without	-	43.17	0.008	Hirashima et al. 1990b
Helicoverpa zea (Boddie)	Noctuidae	*Cardiochiles nigriceps* Vierick	Braconidae	Exposed Larvae	Solitary	With	Cotton	6.19	207.000	Tillman 1996
Helicoverpa zea (Boddie)	Noctuidae	*Microplitis croceipes* (Cresson)	Braconidae	Exposed Larvae	Solitary	With	Cotton	11.20	206.820	Tillman 1996
Helicoverpa zea (Boddie), *Heliothis virescens* (F.)	Noctuidae	*Microplitis croceipes* (Cresson)	Braconidae	Exposed Larvae	Solitary	With	Wild Host Plants	11.16	0.927	Hopper and King 1986
Helicoverpa zea (Boddie), *Heliothis virescens* (F.)	Noctuidae	*Microplitis croceipes* (Cresson)	Braconidae	Exposed Larvae	Solitary	With	Cotton	11.16	7.888	Hopper and King 1986
Plutella xylostella L.	Plutellidae	*Cotesia plutellae* (Kurdjumov)	Braconidae	Exposed Larvae	Solitary	With	Cabbage	33.33	2.825	Mitsunaga et al. 2004
Plutella xylostella L.	Plutellidae	*Diadegma semiclausum* Hellen	Ichneumonidae	Exposed Larvae	Solitary	With	Cabbage	13.60	0.755	Yang et al. 1994
Spodoptera frugiperda (Smith)	Noctuidae	*Ophion flavidus* Brulle	Ichneumonidae	Exposed Larvae	Solitary	With	Peanuts	25.72	0.301	Rohlfs and Mack 1984
Ephestia kuehniella Zeller	Pyralidae	*Bracon hebetor* (Say)	Braconidae	Exposed Larvae	Solitary	Without	-	4.66	0.096	Taylor 1988
Spodoptera frugiperda (Smith)	Noctuidae	*Cotesia marginiventris* (Cresson)	Braconidae	Exposed Larvae	Solitary	Without	-	47.41	0.175	Riggen et al. 1994

Table 4.1. (Continued)

Lepidopteran Host Species	Host Family	Hymenopteran Parasitoid Species	Parasitoid Family	Host Stage and Exposure	Parasitoid Oviposition Pattern	Experimental Arena Complexity (with /without host plants)	Host Plant	Maximum Daily Parasitism per Female	Effective Search Rate (m^2 surface area day^{-1} $parasitoid^{-1}$)	Data Source
Spodoptera litura F.	Noctuidae	*Microplitis prodeniae* (Viereck)	Braconidae	Exposed Larvae	Solitary	Without	-	67.61	0.053	Jiang et al. 2002
Helicoverpa armigera (Hübner)	Noctuidae	*Campoletis chloridae* Uchida	Ichneumonidae	Exposed Larvae	Solitary	Without	-	12.02	0.259	Kumar et al. 1994
Spodoptera frugiperda (Smith)	Noctuidae	*Campoletis grioti* Blanchard	Ichneumonidae	Exposed Larvae	Solitary	Without	-	72.11	0.363	Varone et al. 2007
Spodoptera frugiperda (Smith)	Noctuidae	*Campoletis sonorensis* (Cameron)	Ichneumonidae	Exposed Larvae	Solitary	Without	-	66.98	0.053	Isenhour 1985
Anticarsia gemmatalis Hübner	Noctuidae	*Microcharops anticarsiae* Gupta	Ichneumonidae	Exposed Larvae	Solitary	Without	-	38.00	0.226	Patel and Habib 1993
Cnaphalocrocis medinalis Guenée	Pyralidae	*Apanteles cypris* Nixon	Braconidae	Semi-exposed Larvae	Solitary	With	Rice	9.50	13.905	Wei and Zhao 1991
Cnaphalocrocis medinalis Guenée	Pyralidae	*Cardiochiles philippinensis* Ashmead	Braconidae	Semi-exposed Larvae	Solitary	With	Rice	3.40	1.197	Runjie et al. 1996
Phyllocnistis citrella Stainton	Gracillariidae	*Citrostichus phyllocnistoides* (Narayanan)	Eulophidae	Semi-exposed Larvae	Solitary	With	Mandarin	11.13	1.113	Wang et al. 2006
Tuta absoluta (Meyrick)	Gelechiidae	*Pseudapanteles dignus* (Muesebeck)	Braconidae	Semi-exposed Larvae	Solitary	Without	-	3.01	0.027	Luna et al. 2007
Phyllonorycter cydoniella (Denis and Schiffermüller)	Gracillariidae	*Sympiesis sericeicornis* Nees	Eulophidae	Semi-exposed Larvae	Solitary	Without	-	3.71	0.191	Cacas et al. 1993
Diatraea grandiosella Dyar	Pyralidae	*Allorhogas pyralophagus* Marsh	Braconidae	Concealed Larvae	Gregarious	With	Corn	0.41	0.145	Overholt and Smith 1990
Diatraea saccharalis F.	Crambidae	*Cotesia flavipes* (Cameron)	Braconidae	Concealed Larvae	Gregarious	With	Rice	0.96	0.030	Chapter III
Diatraea saccharalis F.	Crambidae	*Cotesia flavipes* (Cameron)	Braconidae	Concealed Larvae	Gregarious	With	Corn	0.93	0.162	Wiedenmann and Smith 1993
Sesamia calamistis Hampson	Noctuidae	*Cotesia flavipes* (Cameron)	Braconidae	Concealed Larvae	Gregarious	With	Corn	0.41	0.055	Sallam et al. 1999
Chilo partellus (Swinhoe)	Pyralidae	*Cotesia flavipes* (Cameron)	Braconidae	Concealed Larvae	Gregarious	With	Corn	0.69	0.138	Sallam et al. 1999
Diatraea grandiosella Dyar	Pyralidae	*Cotesia flavipes* (Cameron)	Braconidae	Concealed Larvae	Gregarious	With	Corn	0.93	0.006	Overholt and Smith 1990
Sesamia calamistis Hampson	Noctuidae	*Cotesia sesamiae* (Cameron)	Braconidae	Concealed Larvae	Gregarious	With	Corn	0.40	0.057	Sallam et al. 1999
Chilo partellus (Swinhoe)	Pyralidae	*Cotesia sesamiae* (Cameron)	Braconidae	Concealed Larvae	Gregarious	With	Corn	0.30	0.044	Sallam et al. 1999

Table 4.1. (Continued)

Lepidopteran Host Species	Host Family	Hymenopteran Parasitoid Species	Parasitoid Family	Host Stage and Exposure	Parasitoid Oviposition Pattern	Experimental Arena Complexity (with /without host plants)	Host Plant	Maximum Daily Parasitism per Female	Effective Search Rate (m^2 surface area day^{-1} $parasitoid^{-1}$)	Data Source
Diatraea grandiosella Dyar	Pyralidae	*Digonogastra kimballi* Kirkland	Braconidae	Concealed Larvae	Gregarious	With	Corn	1.18	0.380	Overholt and Smith 1990
Eoreuma loftini (Dyar)	Pyralidae	*Allorhogas pyralophagus* Marsh	Braconidae	Concealed Larvae	Gregarious	Without	-	2.30	0.005	Harbison et al. 2001
Sesamia calamistis Hampson	Noctuidae	*Cotesia flavipes* (Cameron)	Braconidae	Concealed Larvae	Gregarious	Without	-	0.69	0.083	Sallam et al. 1999
Chilo partellus (Swinhoe)	Pyralidae	*Cotesia flavipes* (Cameron)	Braconidae	Concealed Larvae	Gregarious	Without	-	0.91	0.050	Sallam et al. 1999
Sesamia calamistis Hampson	Noctuidae	*Cotesia sesamiae* (Cameron)	Braconidae	Concealed Larvae	Gregarious	Without	-	0.65	0.017	Sallam et al. 1999
Chilo partellus (Swinhoe)	Pyralidae	*Cotesia sesamiae* (Cameron)	Braconidae	Concealed Larvae	Gregarious	Without	-	0.65	0.056	Sallam et al. 1999

category was excluded from further analyses because too few data were available. Table 4.2 summarizes leaf, stem, and fruiting structure surface areas of each host plant species used in the functional response studies, while Table 4.3 summarizes the lower temperature threshold, immature developmental duration, adult longevity, number of progeny produced per parasitized host, and sex ratio of each cited parasitoid species, and the corresponding data source.

Although *Trichogramma* spp. are the most widely released parasitoids worldwide, accounting for 97.4% of the 15.5 million ha having received augmentative or inundative releases (van Lenteren 2000), only 9 sets of data (20.9%) from the literature search were for *Trichogramma* spp. The discrepancy between the two percentages is due to a disproportionate number of *Trichogramma* studies not providing estimates of host and parasitoid density, and as a result not being of use in estimating the impact of both factors on maximum daily parasitism per female and effective search rate.

Among the 42 datasets used herein, 7 of the 9 egg parasitoid datasets and all of the exposed and semi-exposed larvae datasets were for solitary parasitoids. In contrast, all datasets for concealed larvae were for gregarious parasitoids. Mayhew (1998) reviewed studies involving 68 hymenopteran parasitoid families and reported the 4 families involved in the analysis presented herein (Braconidae, Eulophidae, Ichneumonidae, and Trichogrammatidae) exhibited both solitary and gregarious parasitoid development. Both gregarious and solitary parasitoids attack each of the host stages and each level of host concealment (Triplehorn and Johnson 2004). Blackburn (1991) investigated how host

Table 4.2. Host plant surface area used to estimate effective search rate

Host Plant	Structure Occupied by the Lepidopteran Host	Plant Age or Growth Stage when Injury Occurs	Plant Surface Area per m^2 Ground Area (m^2)	Data Sources
Cabbage (*Brassica oleracea* L.)	Leaf	6-Weeks Old	6.400	Aquino et al. 2005
Corn (*Zea mays* L.)	Leaf	120-Day Old	7.200	Flesch and Dale 1987
	Stem	120-Day Old	1.002	Foroutan-pour et al. 2000, Echezona 2007
Cotton (*Gossypium hirsutum* L.)	Leaf	Pre-Flowering Stage	9.000	Zhang et al. 2008
	Square	Pre-Flowering Stage	0.023	Wilson and Bishop 1982, Wilson et al. unpublished data
	Bract	Pre-Flowering Stage	0.233	Ritchie et al. 2007
Mandarin (*Citrus reticulata* L.)	Leaf	8-Year Old	5.990	Cohen et al. 2005
Peanut (*Arachis hypogaea* L.)	Leaf	11-Nodes Stage	4.500	Rohlfs and Mack 1985
Rice (*Oryza sativa* L.)	Leaf	40-Day Old -	1.300 9.000	Zhong et al. 2002
	Stem	-	6.004	Lv et al. unpublished data, Wilson unpublished data
Wild Host Plants (chiefly *Geranium dissectum* L.)	Leaf	-	2.600	Dejoux et al. 1999

Table 4.3. Summary of life table parameters for each hymenopteran parasitoid species for which functional response parameters were estimated

Parasitoid Species	Parasitoid Family	Lower Development Threshold (ºC)	Immature Developmental Duration ($\bar{x}$ ± *s.d.*)	Adult Longevity ($\bar{x}$ ± *s.d.*)	Average Number of Progeny Produced per Parasitized Host	Proportion of Female Offspring	Data Source
Allorhogas pyralophagus Marsh	Braconidae	10.7[b]	271.6 ± 75.4	296.8 ± 65.1	3.8	0.50	Melton and Browning 1986
Apanteles cypris Nixon	Braconidae	11.3	228.6 ± 30.3	59.5 ± 33.9	1	0.58	Chen et al. 1983
Bracon hebetor (Say)	Braconidae	10.7[b]	182.4 ± 3.6	536.3 ± 23.8	1	0.64	Nikam and Pawar 1993, Magro and Parra 2001, 2004
Cardiochiles nigriceps Vierick (*Cardiochiles philippinensis* Ashmead)[a]	Braconidae	10.9	487.3 ± 84.5	280.5 ± 76.1	1	0.50	Butler et al. 1983
Cotesia flavipes (Cameron)	Braconidae	10.4	277.4 ± 8.2	69.8 ± 7.3	26.7	0.72	Chapter III
Cotesia marginiventris (Cresson)	Braconidae	10.5	238.9 ± 21.0	120.7 ± 54.9	1	0.60	Kunnalaca and Mueller 1979, Cecilia and Luna 1996
Cotesia plutellae (Kurdjumov)	Braconidae	10.7[b]	124.4 ± 15.6	114.4 ± 14.3	1	0.41	Mitsunaga et al. 2004, Schuler et al. 2004
Cotesia sesamiae (Cameron)	Braconidae	8.5	327.2 ± 23.4	28.0 ± 7.1	22.6	0.63	Alleyne and Wiedenmann 2002
Digonogastra kimballi Kirkland	Braconidae	13.0	260.8 ± 16.0	457.6 ± 102.4	4.6	0.50	Kirkland 1982, Lee and Chippendale 1985
Microplitis croceipes (Cresson)	Braconidae	10.7[b]	263.9 ± 18.6	167.9 ± 24.4	1	0.52	Tillman et al. 1993, Tillman 1994
Microplitis prodeniae (Viereck)	Braconidae	10.6	219.0 ± 20.3	63.4 ± 9.6	1	0.70	Chen et al. 2003
Pseudapanteles dignus (Muesebeck)	Braconidae	10.7[b]	156.9 ± 50.8	344.6 ± 50.8	1	0.56	Luna et al. 2007
Citrostichus phyllocnistoides (Narayanan)	Eulophidae	9.8	212.0 ± 29.1	152.0 ± 45.6	1	0.50	Urbaneja et al. 2003, Rao et al. 2004
Sympiesis marylandensis Girault (*Sympiesis sericeicornis* Nees)[a]	Eulophidae	8.3	160.8 ± 39.6	867.3 ± 328.7	1	0.30	Ridgway and Mahr 1990
Campoletis chloridae Uchida (*Campoletis grioti* Blanchard, *Campoletis sonorensis* (Cameron)) [a]	Ichneumonidae	3.4	280.0 ± 40.1	205.3 ± 56.6	1	0.65	Pandey and Tripathi 2008
Diadegma semiclausum Hellen	Ichneumonidae	6.6	273.3 ± 13.5	311.0 ± 87.4	1	0.50	Abbas 1988, Yang et al. 1993
Microcharops anticarsiae Gupta	Ichneumonidae	5.0[b]	388.1 ± 17.4	459.4 ± 220.4	1	0.29	Patel and Habib 1993, 1998
Ophion flavidus Brulle	Ichneumonidae	5.0[b]	552.5 ± 302.1	236.9 ± 55.2	1	0.09	Rohlfs and Mack 1985
Trichogramma chilonis (Ishii)	Trichogrammatidae	9.8	148.9 ± 4.9	81.0 ± 37.3	1	0.60	Hirashima et al. 1990a, Haile et al. 2002
Trichogramma minutum Riley	Trichogrammatidae	10.2	128.0 ± 7.2	242.7 ± 12.8	1	0.60	Yu et al. 1984, Nordlund et al. 1997
Trichogramma ostriniae Pang and Chen	Trichogrammatidae	10.3	163.2 ± 21.3	54.3 ± 6.9	1.5	0.64	Saljoqi and He 2004
Trichogramma pretiosum Riley	Trichogrammatidae	11.0	126.9 ± 17.1	202.3 ± 12.9	1	0.64	Harrison et al. 1985, Meceda et al. 2003

[a] Life table parameters are not available from the literature, and was estimated using those of the taxonomy similar species within the same genus.

[b] Lower development threshold is not available from the literature, and was estimated using mean for species within the same family used in the present study.

mortality constrains the evolution of parasitoid life-history traits, and hypothesized those parasitoids that attack later stages and concealed hosts have a higher search rate and lower fecundity. However, concealed larvae were attacked most frequently by gregarious parasitoids in the data cited herein. Mayhew (1998) concluded solitary parasitism is an ancestral trait, with transition to gregarious parasitism having occurred numerous times. Rosenheim and Hongkham (1996) suggested a possible scenario for the transition: females lay more than 1 egg per host during a single host visit, with additional parasitoid eggs serving as “insurance eggs” to increase the chance of successful parasitoid emergence. Cornell (1988) indicated gregarious parasitoids show a greater trend toward sib-mating. It is reasonable to assume the lower host density of the latter instars and their concealed niche within stems makes them more difficult to find. Sib-offspring emerging from isolated hosts should exhibit a greater degree of sib-matings, which should accelerate the spread of alleles that code for this gregarious oviposition behavior. However, further studies are required to support this hypothesis.

The maximum daily parasitism per female was significantly affected by host stage/exposure, and was higher for parasitoids that attack eggs and exposed larvae, followed by semi-exposed and concealed larvae (Tables 4.4, 4.5). The effect of host stage/exposure on maximum daily parasitism per female was confounded by parasitoid oviposition strategy, with all parasitoids that attack concealed larvae in this analysis being gregarious, while all but two that attack eggs, exposed, and semi-exposed larvae being solitary. The lower maximum daily parasitism per female of parasitoids that attack concealed larvae was partially due to their gregarious oviposition strategy. Blackburn

Table 4.4. Means for functional response and life table parameters for each parasitoid category analyzed in this study

Parasitoid Oviposition Strategy	Host Stage/Exposure	Experimental Arena Complexity (with/without host plants)	Maximum Daily Parasitism per Female	Effective Search Rate (m^2 surface area female^{-1} day^{-1})	Lower Temperature Developmental Threshold (°C)	Developmental Duration (DD > LDT)	Adult Longevity (DD > LDT)	Proportion of Female Offspring
Solitary	Egg	Without	28.62	0.012	10.3	134.6	175.3	0.61
		With	12.10	0.600				
	Exposed Larvae	Without	44.11	0.175	8.4	301.0	249.6	0.49
		With	19.98	60.931				
	Semi-exposed Larvae	Without	3.35	0.113	9.8	189.6	355.9	0.49
		With	8.00	5.405				
Gregarious	Egg	Without	34.40	0.006	10.3	163.2	54.3	0.64
		With	-	-				
	Concealed Larvae	Without	1.06	0.042	10.6	284.3	213.1	0.59
		With	0.69	0.109				

Table 4.5. ANOVAs for functional response parameters estimated separately for each of the 42 datasets, and life table parameters estimated for each of the 25 parasitoid species contained within

Source of Variances	Maximum Daily Parasitism per Female		Effective Search Rate (m^2 surface area $female^{-1}$ day^{-1})		Lower Temperature Developmental Threshold (°C)		Developmental Duration (DD > LDT)		Adult Longevity (DD > LDT)		Proportion of Female Offspring	
	df	P > F	df	P > F	df	P > F	df	P > F	df	P > F	df	P > F
Host Stage/Exposure	3	0.004	3	0.425	3	0.991	3	0.057	3	0.617	3	0.635
Parasitoid Oviposition Strategy	1	0.624	1	0.999	1	0.719	1	0.808	1	0.621	1	0.882
Experimental Arena Complexity	1	0.056	1	0.291	-	-	-	-	-	-	-	-
Host Stage/Exposure × Host Experimental Arena Complexity	3	0.050	3	0.252	-	-	-	-	-	-	-	-
Error	33		33		10[a]		17[a]		17[a]		17[a]	

[a] Life table parameters estimated from taxonomy similar species were not counted repetitively in ANOVA analyses.

(1991) found no correlation between parasitoid fecundity and parasitoid oviposition strategy.

Although not statistically significant, there is a trend with effective search rate higher when experiments were conducted in arenas with host plants, especially for parasitoids that attack exposed larvae (Table 4.4, 4.5). For experiments cited herein, lepidopteran host density was generally lower when host plants were present. A significant impact of lepidopteran host density on effective search rate was not detected (Table 4.6). However, this does not suggest the area searched by each parasitoid is a constant. The area searched by a parasitoid increases with decreasing host density, approaching the effective search rate.

Host stage/exposure did not have a significant effect on effective search rate, when estimated separately for each of the 42 datasets (Table 4.5). However, when data were combined for all species that attack the same host stage/exposure, the effective search rate was highest for parasitoids that attack semi-exposed larvae, followed by exposed larvae, eggs, and concealed larvae (Table 4.6). Egg parasitoids generally locate hosts using visual and chemical cues, while parasitoids that attack larvae locate their host using visual, acoustic, or chemical cues from host frass or host plant secretions (Turlings et al. 1993). Generally, it is easier for parasitoids to detect physical or chemical cues produced by exposed and semi-exposed hosts than by concealed hosts (Vet et al. 1990). In addition, parasitoids face greater risks in attacking concealed hosts. Some stem borer species do not clean the frass and debris inside their tunnels, and it is difficult for parasitoids to enter and reach the hosts even when cues are detected. Large lepidopteran

Table 4.6. Functional response parameters for each of the five parasitoid categories, with incremental F-test used to measure whether effective search rate is a linear function of host density

Parasitoid Oviposition Strategy	Host Stage/Exposure	*b*	*s*	R^2	F	P > F	Incremental F	P > F
Solitary	Eggs	30.147	0.0377	0.893	400.79	~ 0	0.27	0.604
	Exposed Larvae	30.138	4.2633	0.714	107.48	~ 0	0.01	0.931
	Semi-exposed Larvae	5.367	13.3495	0.720	39.81	~ 0	~ 0	0.991
Gregarious	Eggs	41.359	0.0064	0.949	55.32	~ 0	~ 0	~ 1
	Concealed Larvae	1.137	0.0012	0.689	73.88	~ 0	0.03	~ 1

larvae can be strong defenders and chances for a parasitoid to be killed when attacking increase when parasitism occurs inside a stem. A previous study conducted on parasitism of *D. saccharalis* by *C. flavipes* showed 30%-40% of the parasitoids were killed as a result of biting, spitting, and larval twisting within the tunnels (Potting et al. 1999).

The developmental duration of egg parasitoids was shorter than that of the larval parasitoids (Table 4.4, 4.5). Parasitoid oviposition strategy and host stage/exposure did not have a significant impact on lower developmental threshold, adult longevity, or proportion of female offspring (Table 4.5). Blackburn (1991) analyzed the correlation between parasitoid immature developmental duration and adult longevity, with parasitoid size, parasitoid oviposition strategy, host stage, and host exposure, using 474 hymenoptera parasitoid species in 27 Hymenoptera families. He indicate immature developmental duration is positively correlated with parasitoid size, but adult longevity was not. For comparable sized parasitoids, parasitoid oviposition strategy, host stage, and host concealment did not have a significant impact on either immature developmental duration or adult longevity.

Augmentative Biological Control Simulation Analyses. Maximum daily parasitism per female and effective search rate were both significantly affected by host stage/exposure. However, the analyses do not estimate the impact of these factors on the likely success of augmentative biological control release programs. In this section, I simulate the impact of timing of release for 5 parasitoid categories (solitary parasitoids that attack eggs, exposed larvae, and semi-exposed larvae, and gregarious parasitoids that attack eggs and concealed larvae), on the rate of pest population increase and the putative economic value of releases compared to that achieved using conventional insecticide-based control.

Model Description. Diatraea saccharalis was used as a model host in this simulation analysis. This species exhibits different degrees of host exposure during its immature development, allowing the incorporation of the effect of this variable in the simulation analysis. Eggs are oviposited in clusters on both the top and bottom surfaces of leaves (Dale 1994). The 1st instars disperse to leaf sheaths where they feed on the surface. Second and 3rd instars move between the leaf sheaths and stems where they are partially concealed. Third instars begin to feed on and burrow into stems, with 4th and latter instars found entirely within stems (Capinera 2001). *Diatraea saccharalis* is a pest of broad economic importance to a number of cultivated monocots across a large area of the U.S. Gulf Coast (Bessin and Reagan 1990, Way et al. 2006). Rice was chosen as the host crop due to its economic importance (Stansel and Tate 2005, Falconer 2008), and the author's previous experience studying the impact of *D. saccharalis* on rice, as affected by a number of factors including augmentative parasitoid releases (Lv et al. 2008, Chapter III).

The population dynamics of *D. saccharalis* and each of the 5 parasitoid categories were simulated using the cohort-based age-structured model developed by Lv (Chapter III). This model uses a physiological time scale (degree-days > the lower developmental threshold), with population progressions calculated daily. The lower developmental threshold is 10.4˚C for *D. saccharalis* (Chapter III), with an averaged estimate for each parasitoid category listed in Table 4.4. The development of each species is simulated using a distributed maturation algorithm. The parasitoid life table parameters used in the simulations were derived from the means of the main effects for the corresponding ANOVA's described in the previous section (Table 4.4).

The *D. saccharalis* model was initiated with overwintering larvae at the time of diapause termination in early spring. Population progression was simulated in rice through the main crop, and in the stubble as larvae and pupae, where they remain until next year's spring adult emergence. Simulation of overwintering larvae provides estimates of the timing of larval diapause termination, subsequent pupal development, and adult emergence each following spring. Intrinsic survivorship of *D. saccharalis* was simulated as a function of temperature, while extrinsic survivorship was simulated as a function of host plant age, rainfall, and parasitism (Chapter III). To estimate daily parasitism, unit area densities of both *D. saccharalis* and the parasitoid were converted to density per m^2 surface area for use in the Frazer-Gilbert equation. Surface area estimates for rice consist of two components, leaf surface area and stem surface area. Estimates for both parameters were obtained from Wu and Wilson (unpublished data). Maximum daily parasitism per female and effective search rate for each parasitoid category are summarized in Table 4.6.

The immigration and emigration of *D. saccharalis* moths were assumed to be equal. Parasitoid population progression was simulated from the timing of augmentative release to the last generation each year. Parasitism per day was simulated based on host and parasitoid density, maximum daily parasitism per female, and effective search rate, using the Frazer-Gilbert functional response equation (Frazer and Gilbert 1976).

The economic value of each potential parasitoid augmentative release was estimated for each overwintering larval density, each timing of release, and each year, as the difference between the value of the yield loss prevented (Y_p) and the cost of the release (Eq. 4.4a). The yield loss prevented by parasitoid release was estimated as the difference in yield with and without parasitoid release, with yield a function of simulated generational cumulative density of 3rd and later *D. saccharalis* instars (Eqs. 4.4b-e from Chapter III).

$$E = vY_p - c \tag{4.4a}$$

$$\begin{aligned} Y_1 = {} & -5.14 + 0.0191DD_r - 0.00000199\rho_i - 0.0000150DD_r^{\,2} \\ & + 0.00000000343DD_r\rho_i - 0.00000000000199\rho_i^{\,2} \end{aligned} \tag{4.4b}$$

$$\begin{aligned} Y_2 = {} & -0.581 + 0.00290DD_r + 0.000000418\rho_i - 0.00000137DD_r^{\,2} \\ & - 0.000000000508DD_r\rho_i \end{aligned} \tag{4.4c}$$

$$\begin{aligned} Y_3 = {} & -3.05 + 0.00570DD_r - 0.000000398\rho_i - 0.00000192DD_r^{\,2} \\ & + 0.000000000000155\rho_i^{\,2} \end{aligned} \tag{4.4d}$$

$$Y = Y_u \prod_{i=1}^{3} Y_i \tag{4.4e}$$

where:

E = Economic value of parasitoid release (\$ ha^{-1})

v = Market value of the crop per unit of product (\$0.418 kg^{-1}, Chicago Board of Trade Jan. 2009 futures price estimated on Aug. 28, 2008)

Y_p = Yield loss prevented by parasitoid release (kg ha^{-1})

c = Cost of pest control (\$ ha^{-1})

Y_i = Relative yield as affected *D. saccharalis* larvae for the i^{th} generation

DD_r = Degree-days (> 10°C) from rice planting to the time when injury occurred

ρ_i = Cumulative density (ha^{-1}) of *D. saccharalis* larvae reaching the 3^{rd} instar for the i^{th} generation

Y = Rice yield (kg ha^{-1}) as affected by three generations of *D. saccharalis* injury

Y_u = Yield in the absence of *D. saccharalis* injury (6,776.4 kg ha^{-1}, derived from Lv et al. 2008)

Simulation Scenarios. Five sets of simulations were conducted, representing the five parasitoid categories. For each category, ten overwintering diapausing *D. saccharalis* larvae densities were simulated, ranging from 1 to 10 larvae m^{-2}, with the highest density corresponding to the highest previously observed *D. saccharalis* diapausing larval infestation, where natural enemies have been eliminated by the use of broad-spectrum insecticides (Bessin and Reagan 1993). The effect of the timing of parasitoid release was simulated in 10-day increments from 30 days after rice planting in the spring to main crop harvest. For each parasitoid, one release density was simulated, corresponding to the cost of two gamma-cyhalothrin (Prolex™), lambda-cyhalothrin (Karate Z®), or zeta-cypermethrin (Mustang MAX™) applications (\$67.00 ha^{-1}). Two insecticide applications are usually applied to prevent *D. saccharalis* from causing economic loss during main crop development. Approximately 70,000 egg parasitoids ha^{-1} or 5,700 larval parasitoids ha^{-1} can be reared, shipped, and released at this cost. This assumes the cost of using an egg parasitoid is equal to that of *Trichogramma ostriniae* Pang and Chen (Hymenoptera: Trichogrammatidae), and the cost of using a larval parasitoid is equal to that of *C. flavipes*. The costs for rearing, shipping, and releasing this number of *T. ostriniae* are \$35.05 ha^{-1} (M. P. Hoffman personal communication), \$0.23 ha^{-1} (S. Penn personal communication), and \$31.72 ha^{-1} (S. Penn personal communication), respectively. The corresponding costs for *C. flavipes* are \$41.56 ha^{-1} (D. G. Hall personal communication), \$0.16 ha^{-1} (R. V. Dowell personal communication), and \$25.28 ha^{-1} (S. Penn personal communication). These estimates assume a minimum of 650 ha of rice receive an augmentative release, ca. equal to the annual hectarage planted for a moderate size rice farming operation in Texas.

Each simulation was continued for 31 years, using 1977 to 2007 climate data for Beaumont, Texas, obtained from the *iAIMS* climatic database (Wilson et al. 2007), with the first year's climatic data providing an estimate of the timing of initiation of diapause termination, and the subsequent 30 years providing estimates of *D. saccharalis* and parasitoid population dynamics, as affected by year to year climatic variability.

ANOVAs were conducted on simulated seasonal cumulative damaging larval density, seasonal maximum proportion host parasitized, seasonal maximum parasitoid density, yield, and economic value of each release, each as affected by year, parasitoid category, overwintering larval density, timing of parasitoid release, and the associated 2-way and 3-way interactions. Year was assumed to be a blocking factor and therefore interactions with year were not examined. The error term for each analysis was calculated as the remaining residual variance divided by the residual degrees of freedom (Kuehl 2000). Results for each ANOVA were expressed as $\bar{x} \pm s.d.$ Main factors or interactions with $P < 0.05$ were considered to be statistically significant.

Population and Economic Value. The impact of each main factor and interaction for each of the 5 response variables are listed in Table 4.7. All response variables were significantly affected by all main factors and interactions. Year resulted in a 26.2-fold range in seasonal cumulative damaging larval density, contributing 43.0% to the total variability, with the highest mean (679.1 ± 505.9 m^{-2}) simulated in 1978, and the lowest (25.9 ± 15.9 m^{-2}) in 1998. Differences in seasonal cumulative damaging larval density across years were due to the effect of winter temperatures on timing of larval diapause termination. Winters with lower temperatures resulted in later adult emergence, while winters with higher temperatures resulted in earlier adult emergence. The earlier the adult emergence, the lower the survival of resulting first generation larvae (Chapter III).

Seasonal maximum proportion host parasitized, seasonal maximum parasitoid density, yield, and economic value were significantly correlated with seasonal cumulative damaging larval density (Table 4.8). Year contributed the greatest variability for seasonal maximum parasitoid density, yield, and economic value (Table 4.7). Yield was greatly reduced in years with higher seasonal cumulative damaging larval density. With the same release rate, a larger number of hosts were parasitized in years with higher host densities, which resulted in faster parasitoid population increase, greater host

Table 4.7. ANOVAs for simulated seasonal cumulative damaging larval density, seasonal maximum proportion host parasitized, seasonal maximum parasitoid density, yield, and economic value from augmentative parasitoid release

Source of Variance	df	Seasonal Cumulative Damaging Larval Density (m^{-2})			Seasonal Maximum Proportion Host Parasitized			Seasonal Maximum Parasitoid Density (m^{-2})			Yield (kg ha^{-1})			Economic value ($ ha^{-1})		
		F	P > F	% Variability Explained	F	P > F	% Variability Explained	F	P > F	% Variability Explained	F	P > F	% Variability Explained	F	P > F	% Variability Explained
Year	29	772.2	~ 0	43.0	34.8	~ 0	0. 8	55.2	~ 0	8.7	852.6	~ 0	40.8	138.6	~ 0	11.2
Parasitoid Category	4	859.4	~ 0	6.6	20517.1	~ 0	63.0	247.0	~ 0	5.4	1519.0	~ 0	10.0	2054.0	~ 0	22.9
Overwintering Larval Density	8	959.4	~ 0	16.6	72.3	~ 0	0.5	57.3	~ 0	2.8	1119.1	~ 0	16.6	199.1	~ 0	5.0
Timing of Release	9	23.5	~ 0	1.6	59.7	~ 0	1.7	23.6	~ 0	4.6	25.3	~ 0	1.5	34.2	~ 0	3.4
Parasitoid Category × Overwintering Larval Density	32	179.7	~ 0	2.8	1871.6	~ 0	11.5	49.2	~ 0	2.1	289.1	~ 0	3.8	390.9	~ 0	8.7
Parasitoid Category × Timing of Release	36	47.6	~ 0	2.9	486.7	~ 0	12.0	16.2	~ 0	2.8	82.4	~ 0	4.4	111.4	~ 0	9.9
Overwintering Larval Density × Timing of Release	72	6.8	~ 0	0.9	7.8	~ 0	0.4	3.5	~ 0	1.4	7.0	~ 0	0.8	9.5	~ 0	1.9
Parasitoid Category × Overwintering Larval Density × Timing of Release	288	1.6	~ 0	0.8	3.7	~ 0	0.8	1.6	~ 0	0.9	1.7	~ 0	0.8	2.3	~ 0	1.8
Error	13028															
Total	13499															

Table 4.8. Correlation between simulated seasonal cumulative damaging larval density, seasonal maximum proportion host parasitized, seasonal maximum parasitoid density, yield, and economic value from augmentative parasitoid release

	Seasonal Cumulative Damaging Larval Density (m^{-2})	Seasonal Maximum Proportion Host Parasitized	Seasonal Maximum Parasitoid Density (m^{-2})	Yield (kg ha^{-1})	Economic value ($ ha^{-1})
Seasonal Cumulative Damaging Larval Density (m^{-2})	-	0.7635	0.9711	-0.9778	0.8311
Seasonal Maximum Proportion Host Parasitized		-	0.6776	-0.8160	0.8584
Seasonal Maximum Parasitoid Density (m^{-2})			-	-0.9111	0.7114
Yield (kg ha^{-1})				-	-0.9095
Economic value ($ ha^{-1})					-

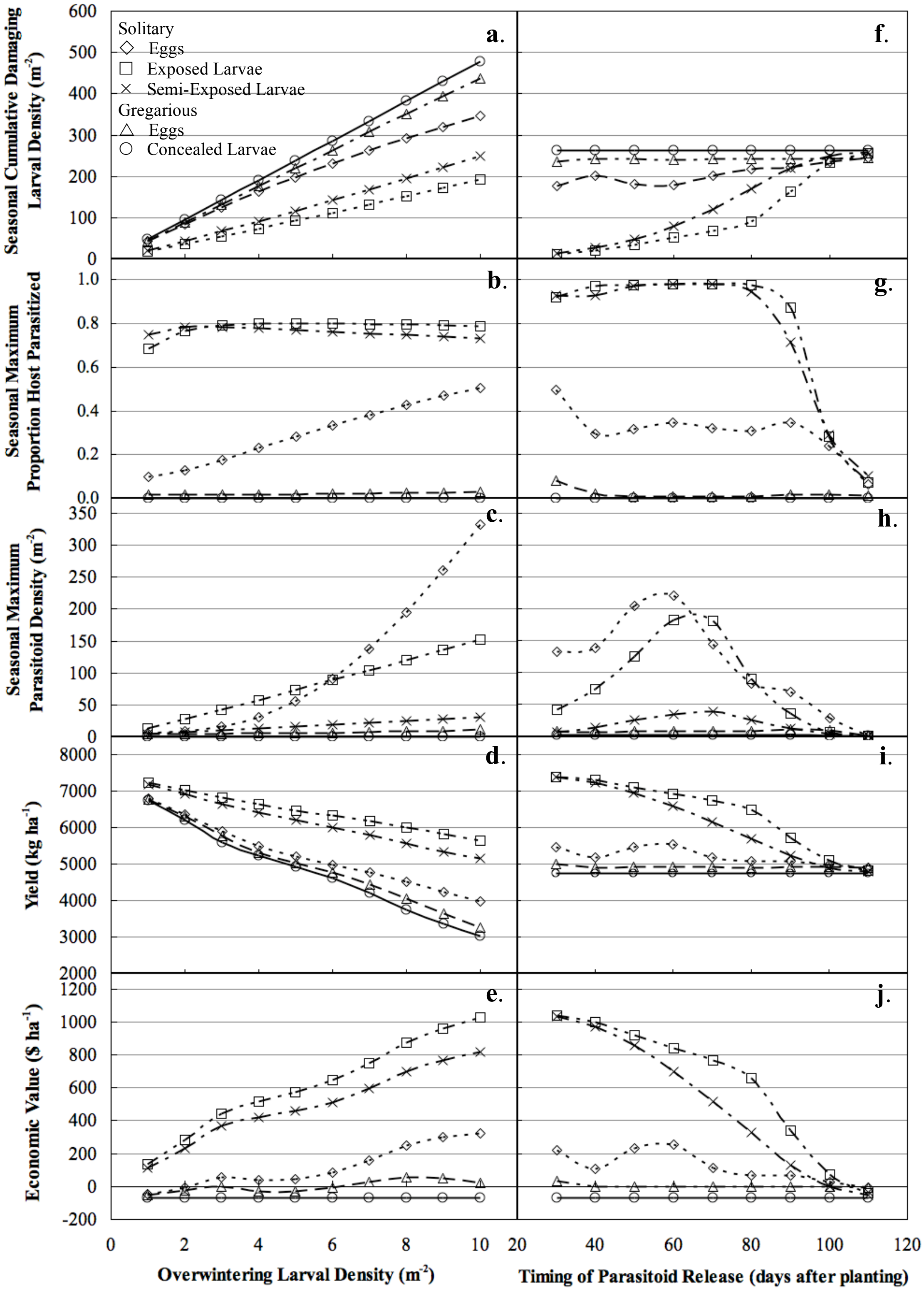
population reduction, and higher economic value. In contrast, year contributed only 0.8% to the variability in seasonal maximum proportion host parasitized, with the highest mean simulated in 1987 (0.438 ± 0.458) and the lowest in 1998 (0.234 ± 0.396). Seasonal maximum proportion host parasitized increased with increasing parasitoid density and decreasing host density. In the present study, a higher proportion host parasitized was generally observed in years with higher host and parasitoid densities.

Among the 5 parasitoid categories, the highest seasonal cumulative damaging larval density (262.4 ± 292.5 m^{-2}) was simulated for gregarious parasitoids that attack concealed larvae, followed by gregarious parasitoids that attack eggs (241.1 ± 257.5 m^{-2}), solitary parasitoids that attack eggs (206.2 ± 195.0 m^{-2}), semi-exposed larvae (131.8 ± 214.7 m^{-2}), and exposed larvae (103.2 ± 183.1 m^{-2}). In contrast, the lowest seasonal maximum parasitoid density was simulated for gregarious parasitoid that attack concealed larvae (0.7 ± 0.2 m^{-2}), followed by gregarious parasitoids that attack eggs (6.7 ± 9.4 m^{-2}), solitary parasitoids that attack semi-exposed larvae (17.5 ± 25.3 m^{-2}), exposed larvae (81.5 ± 135.4 m^{-2}), and eggs (113.2 ± 400.6 m^{-2}). Host availability for parasitoids that attack earlier stages was greater than for those that attack later stages. As a result, a larger number of hosts were parasitized when attacked during earlier stages, which resulted in a more rapid increase in parasitoid population size. However, because rainfall and wind cause a relatively large amount of *D. saccharalis* egg and early larval mortality, parasitism during these stages does not have as great of an effect on host mortality, contrasted with parasitism occurring during later stages.

The lowest seasonal maximum proportion host parasitized (ca. 0), lowest yield (4,760.2 ± 2,291.5 kg ha^{-1}), and lowest economic value (-\$66.62 ± 0.89 ha^{-1}) were simulated for gregarious parasitoids that attack concealed larvae, followed by gregarious parasitoids that attack eggs (0.021 ± 0.029, 4,927.1 ± 2,165.6 kg ha^{-1}, \$3.34 ± 152.06 ha^{-1}), solitary parasitoids that attack eggs (0.303 ± 0.312, 5,211.2 ± 1,853.5 kg ha^{-1}, \$122.36 ± 372.04 ha^{-1}), semi-exposed larvae (0.761 ± 0.349, 6,111.3 ± 1,842.8 kg ha^{-1}, \$499.49 ± 716.39 ha^{-1}), and exposed larvae (0.781 ± 0.353, 6,405.7 ± 1,587.8 kg ha^{-1}, \$622.85 ± 774.73 ha^{-1}). Solitary parasitoids that attack exposed or semi-exposed larvae showed the greatest potential for successful augmentative biological control. In the present study, the release rate used for the egg parasitoids was 12.2 folder higher than that for the larval parasitoids. The lower release rate for larval parasitoids was due to higher cost of augmentative release, which was mainly contributed by higher host rearing cost. The rearing cost can be reduced if parasitoids can be reared in vitro instead of in vivo. Successful in vitro rearing of egg parasitoids, especially *Trichogramma* spp., has been reported (Grenier and Bonnot 1988, Nordlund et al. 1997, Cônsoli and Parra 1999). Successful in vitro rearing of larval parasitoids has also been reported, but only for a limited number of taxonomic groups (Magro and Parra 2004). All successful cases of in vitro parasitoid rearing are for idiobiont parasitoids, whose hosts cease to develop following parasitization (Cônsoli and Parra 1999). The nutritional environment for idiobiont parasitoids to complete their development is relatively stable, with very little physiological or biochemical change. In contrast, hosts of koinobiont parasitoids continue to develop following parasitization, and the physiological and biochemical environment continues to change. It is difficult to mimic the changing environment and food source, required for parasitoid development, using artificial diets. The rearing costs of idiobiont larval parasitoids that can be reared in vitro is lower than that of *C. flavipes*, a koinobiont parasitoid.

Seasonal cumulative damaging larval density, seasonal maximum parasitoid density, seasonal maximum proportion host parasitized, and economic value increased with increasing overwintering larval density, while yield decreased with increasing overwintering larval density. Seasonal cumulative damaging larval density increased the fastest with increasing overwintering larval density for gregarious parasitoids that attack concealed larvae, followed by gregarious parasitoids that attack eggs, solitary parasitoids that attack eggs, semi-exposed larvae, or exposed larvae (Fig. 4.1a). For solitary

Fig. 4.1. Impact of simulated overwintering *D. saccharalis* larval density (a-e) and timing of parasitoid release (f-j) on seasonal cumulative damaging larval density, seasonal maximum proportion host parasitized, seasonal maximum parasitoid density, yield, and economic value, for each parasitoid category.


Solitary
◇ Eggs
□ Exposed Larvae
× Semi-Exposed Larvae
Gregarious
△ Eggs
○ Concealed Larvae
a.
b.
c.
d.
e.
f.
g.
h.
i.
j.
Seasonal Cumulative Damaging Larval Density (m^{-2})
600
500
400
300
200
100
0
Seasonal Maximum Proportion Host Parasitized
1.0
0.8
0.6
0.4
0.2
0.0
Seasonal Maximum Parasitoid Density (m^{-2})
350
300
250
200
150
100
50
0
Yield (kg ha^{-1})
8000
7000
6000
5000
4000
3000
2000
Economic Value ($ ha^{-1})
1200
1000
800
600
400
200
0
-200
0
2
4
6
8
10
20
40
60
80
100
120
Overwintering Larval Density (m^{-2})
Timing of Parasitoid Release (days after planting)

parasitoids that attack eggs, seasonal maximum proportion hosts parasitized increased with increasing overwintering larval density. For solitary parasitoids that attack exposed or semi-exposed larvae, seasonal maximum proportion host parasitized increased at the 3 lowest overwintering larval densities, and showed a trend of decreasing at higher densities. For gregarious parasitoids that attack eggs or concealed larvae, seasonal maximum proportion host parasitized showed an increasing trend with increasing overwintering larval density, but did not differ significantly (Fig. 4.1b).

Seasonal maximum parasitoid density increased the fastest with increasing overwintering larval density for solitary parasitoids that attack eggs, followed by solitary parasitoids that attack exposed larvae or semi-exposed larvae, and gregarious parasitoids that attack eggs or concealed larvae (Fig. 4.1c). Gregarious parasitoids that attack concealed larvae resulted in the greatest yield reduction and least economic value, at all densities, followed by gregarious parasitoids that attack eggs, solitary parasitoids that attack eggs, semi-exposed larvae, and exposed larvae (Fig. 4.1d-e). Positive economic value was observed for solitary parasitoids that attack exposed or semi-exposed larvae at all overwintering larval densities, for solitary egg parasitoids at the 8 highest densities, and for gregarious egg parasitoids at the 4 highest densities. A positive economic value was not observed for gregarious parasitoids that attack concealed larvae.

Seasonal maximum proportion host parasitized was not significantly affected by timing of release for the six earliest dates. In contrast, the three latest dates were significantly less than the earlier dates and from each other. Earlier releases resulted in lower seasonal cumulative damaging larval density, higher yield, and higher economic value. When 1st generation *D. saccharalis* population increase was reduced by parasitism, both host and parasitoid density remained at low levels for the remainder of the season. The highest seasonal maximum parasitoid density was observed when parasitoids were released at the 2nd generation. When parasitoids were released during the 3rd generation, lower parasitoid densities were observed due to limited time for parasitoid population increase.

The parasitoid category × timing of release interaction for each of the 5 response variables is displayed in Fig. 4.1f-j. Timing of release had the greatest impact on seasonal maximum proportion host parasitized for solitary parasitoids that attack exposed or semi-exposed larvae (Fig. 4.1g). For these parasitoid categories, earlier release resulted in lower seasonal cumulative damaging larval density, higher yield, and higher economic value (Fig. 4.1f, i, j). Positive economic value was observed except for the latest release. The highest seasonal maximum parasitoid density was observed when parasitoids were released ca. 60 to 70 days following planting (Fig. 4.1h). For solitary parasitoids that attack eggs, the impact of timing of release on each response variable was similar to that for solitary parasitoids that attack exposed or semi-exposed larvae, but lower parasitism and lower economic value were observed (Fig. 4.1f-j). The highest seasonal maximum parasitoid density was observed when this category of parasitoids was released ca. 60 days after planting. The shorter developmental duration and lower developmental variability of egg parasitoids resulted in major asynchrony between egg parasitoid adult emergence and host egg availability for releases that occurred 40 and 50 days after planting, resulting in lower parasitism rates. For gregarious parasitoids that attack eggs or concealed larvae, timing of release did not significantly affect any of the 5 response variables (Fig. 4.1f-j).

The interactions between overwintering larval density × timing of release contributed the least amount of variability among all 2-way interactions (Table 4.7). Generally, higher seasonal cumulative damaging larval densities were observed at higher overwintering larval densities, with later parasitoids release (Fig. 4.2a). Similarly, except for the two latest releases, higher seasonal maximum proportions host parasitized were detected at higher overwintering larval densities. In contrast, seasonal maximum proportions host parasitized did not differ significantly across overwintering larval densities for the 2 latest releases (Fig. 4.2b). For each overwintering larval density, the highest seasonal maximum parasitoid density was observed when parasitoids were released during the 2nd host generation (Fig. 4.2c). Yield was higher at lower overwintering larval densities, and with earlier parasitoids releases (Fig. 4.2d). Economic value was higher at higher overwintering larval densities and earlier parasitoids releases (Fig. 4.2e). A positive economic value was observed at all overwintering larval densities, except for the three latest releases.

For an augmentative release to be commercially adopted on a broadscale, its economic benefit must be comparable to that achieved using conventional insecticide-based control. Way et al. (2006) reported whitehead tillers, which are symptomatic of *D. saccharalis* injury, was reduced by 87.6% with 2 applications of insecticides, one

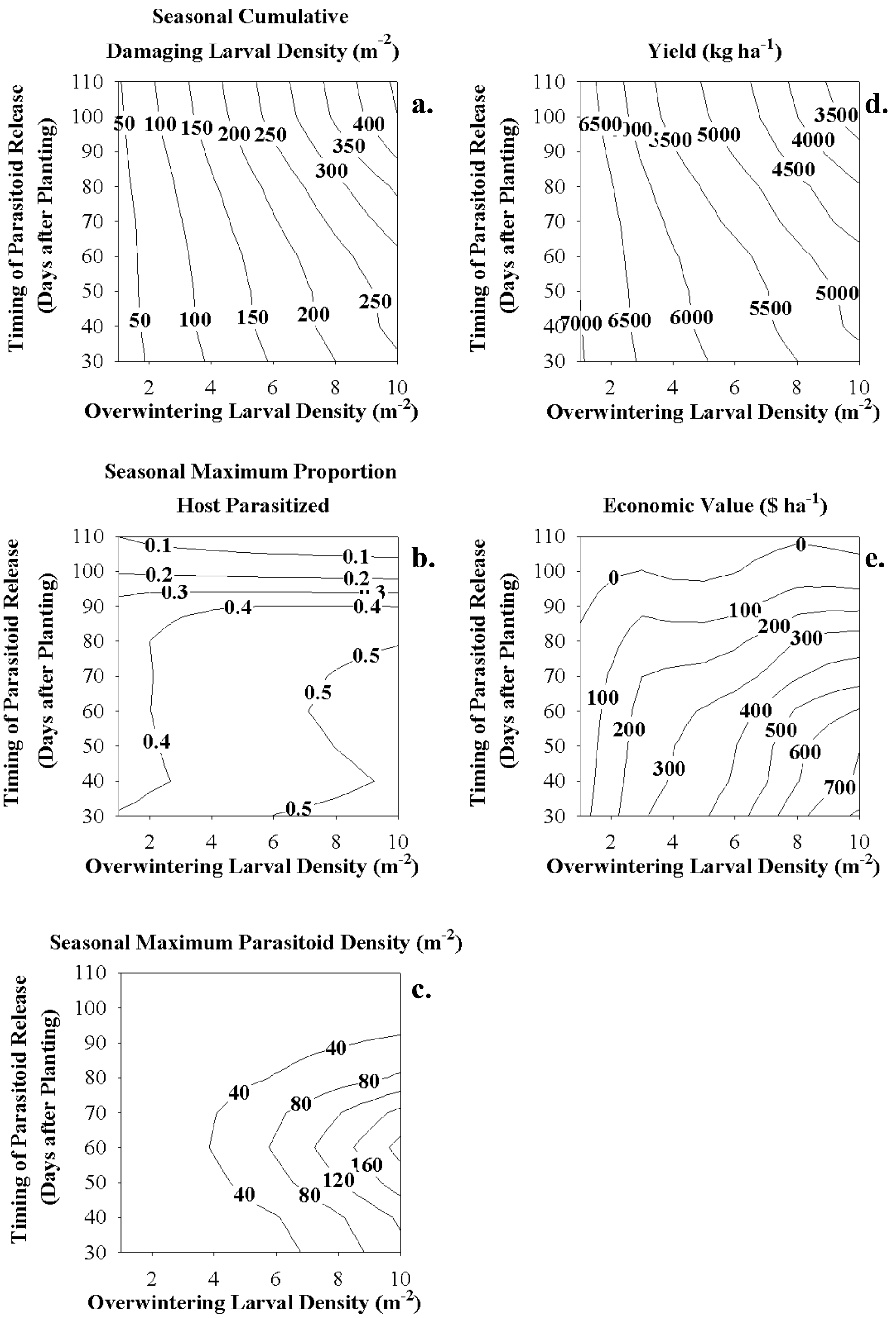


Fig. 4.2. Impact of simulated overwintering *D. saccharalis* larval density and timing of parasitoid release on a) seasonal cumulative damaging larval density, b) seasonal maximum proportion host parasitized, c) seasonal maximum parasitoid density, d) yield, and e) economic value.

each at 1” to 2” panicle and early heading. Reay-Jones et al. (2007) assumed the reduction in *D. saccharalis* injury due to insecticide-based control was proportional to the reduction in whitehead injury. If this assumption is correct, insecticide-based control resulted in \$193.83 to \$1,428.69 ha^{-1} economic benefit when overwintering larval density increased from 1 to 10 m^{-2}. Figure 4.3 summarizes the economic value achieved using either insecticide-based control, and for augmentative releases 30 days after planting. Solitary parasitoids that attack exposed or semi-exposed larvae showed the greatest potential for use in an augmentative biocontrol program, and achieved an average of 122.4% of the economic benefit provided by conventional insecticide-based control, when released 30 days after planting. Augmentative releases of these parasitoids were also economically superior to insecticide-based control when released 40 and 50 days after planting, but the economic benefit was not as great. In contrast, solitary egg parasitoids provided an average of 42.2% of the economic benefit provided by insecticide-based control, when released 30 days after planting, while gregarious parasitoids that attack eggs and concealed larvae provided almost no positive economic value. The simulated economic value provided by parasitoids that attack eggs or concealed larvae in the present study was lower than that estimated by Lv (Chapter III) for *Trichogramma galloi* Zucchi (Hymenoptera: Trichogrammatidae), and *C. flavipes*, respectively, due in both cases to the average effective search rate estimated herein being lower than for either of these parasitoid species. These differences suggest parasitoids of

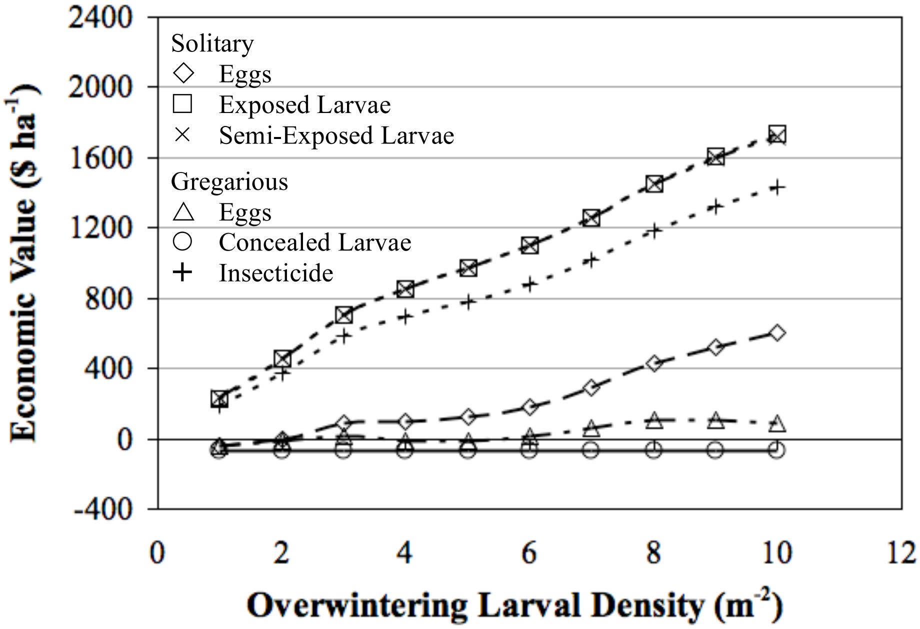


Fig. 4.3. The simulated economic value using either insecticide-based control applied during 1” to 2” panicles and early heading, or each of 5 parasitoids categories augmentatively released 30 days after planting.

eggs or concealed larvae exist that could provide greater economic value when used as part of an augmentative release program. However, Lv (Chapter III) also concluded these parasitoids do not provide economic value comparable to insecticide-based control.

Overall, yield and economic value were both positively correlated with seasonal maximum proportions host parasitized, and explained 9.4% and 39.6% of the total variability in yield and economic value, respectively. However, only 3.6% (480) of the simulations provided an economic value greater than that achieved using insecticide-based control. All 480 simulations were for solitary parasitoids that attacked exposed or semi-exposed larvae. Generally, a greater economic value was observed at high overwintering larval densities and early release dates (Fig. 4.4a-b). Batra (1982) indicates that more than 90% of augmentatively released biocontrol agents either fail to establish or fail to provide economic control. An important question is when do augmentative releases provide an advantage over insecticide-based control?

Conclusions

Herein, I investigated the effects of a number of factors on functional response parameters for hymenopteran parasitoids that attack lepidopteran pests. The maximum daily parasitism per female was highest for solitary parasitoids that attack exposed larvae, followed by solitary and gregarious parasitoids that attack eggs, solitary parasitoids that attack semi-exposed larvae, and gregarious parasitoids that attack concealed larvae. There is a trend with effective search rate being higher when experiments were conducted in arenas with host plants, compared to arenas without host plants.

The simulation analysis suggests augmentative biological control had greater economic value at higher overwintering larval densities and with earlier releases. Solitary parasitoids that attack exposed or semi-exposed larvae provided greater economic benefit than insecticide-based control, for the three earliest releases. Solitary egg parasitoids maintained the host population at sub-economic injury levels, but less economic benefit was provided than insecticide-based control. Gregarious parasitoids that attack eggs and concealed larvae showed the least potential for successful augmentative biological control. Four-hundred and eighty (3.6%) of the simulations provided greater economic value than insecticide-based control, all of which used solitary parasitoids that attacked exposed or semi-exposed larvae.

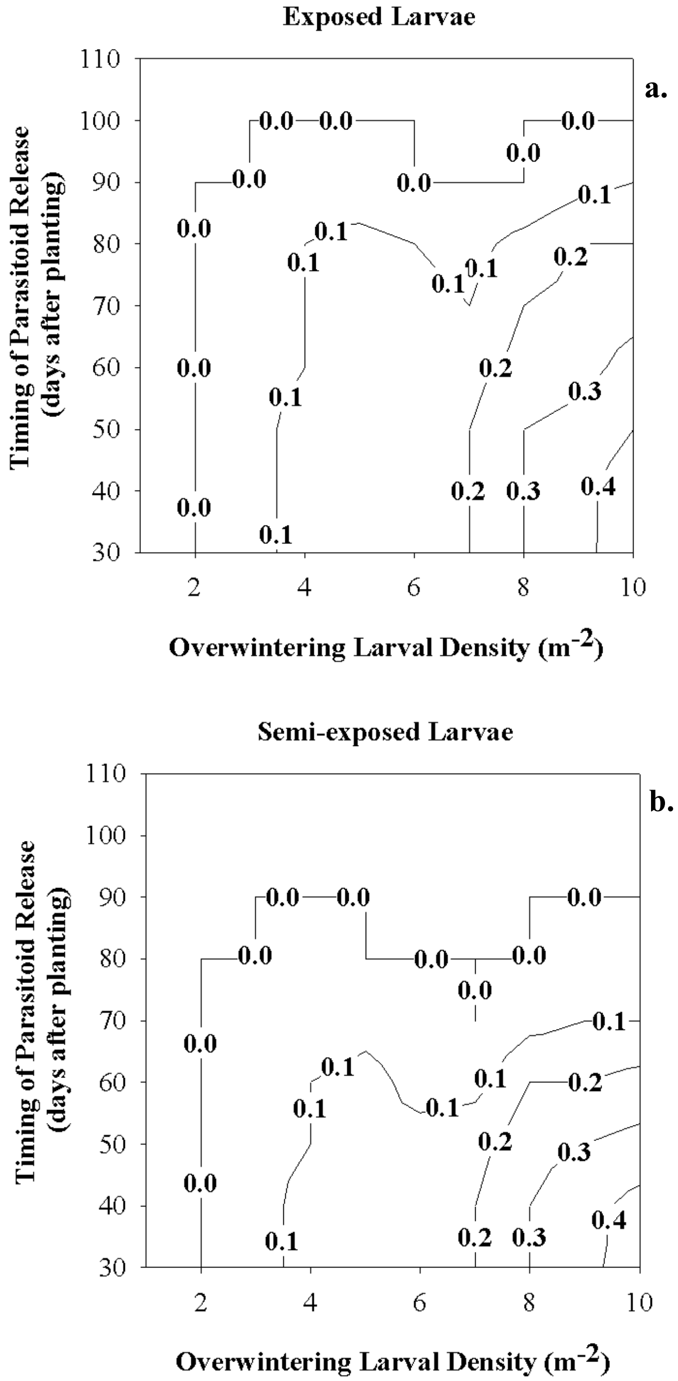


Fig. 4.4. Proportion of simulated augmentative releases that provide a greater economic value than insecticide-based control, using solitary parasitoids that attack a) exposed or b) semi-exposed larvae at each overwintering larval density and release rate.

This analysis is for a lepidopteran host whose parasitoids do not overwinter successfully or that exhibit temporal or spatial asynchrony early in the spring. The results suggest augmentative biological control is only effective for this situation for solitary parasitoids that attack either exposed or semi-exposed larvae. Batra (1982) demonstrated the low probability of successful augmentative biological control releases. The analyses presented herein identify potential reasons for a low level of success and situations when success is more likely. If rearing, shipping and release costs were lower, possible through future improvements with in vitro rearing, the economic feasibility of using some of the parasitoid categories studied herein could be greatly improved. Likewise, for parasitoids that become naturalized in an area, and that overwinter in high numbers, the results would be very different in that augmentative releases could focus on groups of parasitoids that complement the overwintering parasitoid species by attacking other host stages.

CHAPTER V

SUMMARY

Herein, I investigated the response of rice to sugarcane borer injury, and identified 2 mechanisms of tolerance/compensation: rice plants with stem injury producing additional tillers, and tillers with leaf and leaf sheath injury producing large panicles. Our results suggest rice can tolerate and compensate for a relatively high level of stem borer injury. The greatest potential for compensation was observed when injury occurred at panicle differentiation. During this stage, a maximum of 42% of tiller injury and 17% of stem injury can be compensated.

I also investigated the potential value of *C. flavipes* as an augmentatively released agent for biocontrol of the sugarcane borer on rice. Although successful biological control using *C. flavipes* have been reported in tropic areas, my study showed the maximum simulated economic benefit provided by this species was ca. 7.8% of that provided by conventional insecticide-based control. The inability of *C. flavipes* when used augmentatively in temperate-subtropical areas is due to its high rearing cost, a low effective search rate, a low maximum rate of parasitism per female, and both spatial and temporal asynchrony of parasitoid emergence with larval hosts.

Theoretical analyses were conducted to explore whether solitary or gregarious parasitoids that attack different host stage/exposure may produce successful augmentative biocontrol of lepidopteran pests in climatic regions where they were unable to overwinter or exhibit temporal and spatial asynchrony with hosts in early spring. Simulation results show solitary parasitoids that attack exposed or semi-exposed larvae provided greater economic benefit than insecticide-based control, for the three earliest release timings. Solitary egg parasitoids maintained the host population at sub-economic injury levels, but with a less positive economic value than with insecticide-based control. Gregarious parasitoids that attack eggs or concealed larvae provided the lowest economic value.

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